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A MANUAL OF DENTAL ANATOMY

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A MANUAL
OF
DENTAL ANATOMY
HUMAN AND COMPARATIVE

BY

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Sir CHARLES S. TOMES, Kt.
LL.D., F.R.S., F.R.C.S.

EIGHTH EDITION

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PREFACE TO THE EIGHTH EDITION

THE European War has waged over the greater part of the period since the publication of the seventh edition of Sir Charles S. Tomes' well-known manual. This has had its influence in diminishing the output of new investigations into the structure and comparative morphology of the teeth, hence the amount of new material now to be incorporated is less than it might otherwise have been.

The arrangements of the subject-matter adopted in the previous edition have been adhered to in the present. The description of the human teeth has been amplified, and in this I have received much valuable help from Mr. Bowdler Henry, as well as in the chapters dealing with histology; to him my best thanks are cordially given.

It is hoped that the fuller description of the human teeth may render the book of greater value to the dental student, and even of some assistance to the anthropologist.

I should like also to tender my sincere thanks to Mr. A. W. Bell, a student of the Royal Dental Hospital, for the original drawings, made from the teeth themselves, which illustrate Chapter I. I also have to thank Miss D. B. Crofts, B.Sc., Demonstrator of Zoology at Bedford College, University of London, for the somewhat tedious but very necessary work of compiling the index, which she has done with great care.

H. W. MARETT TIMS.

LONDON.

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A

MANUAL OF DENTAL ANATOMY

HUMAN AND COMPARATIVE.

INTRODUCTION.

The range of the subject of Dental ~~Anatomy~~ turns upon the meaning which is attached to the word "tooth"; but although this chapter might most appropriately open with a definition of this word, if such were possible, it is very much easier to explain what is ordinarily understood by it, than to frame any single sentence which shall fulfil the requirements of logical definition. Most vertebrate and a great many invertebrate animals have certain hard masses in or near to the entrance of the alimentary canal, *i.e.*, the mouth. By these hard masses, sometimes of a bony, sometimes of a horny or even of a calcified nature, various offices in connection with the prehension or comminution of food are performed, and to them the term "teeth" is applied. Whilst, however, in some animals these functions are performed by corneous structures throughout life, recent researches have shown that these may sometimes at first underlie and subsequently replace true calcified teeth, as in *Ornithorhynchus*, in other cases horny plates overlie and bury rudimentary calcified teeth. In many animals, teeth have come to be used for purposes other than those of nutrition, such as for sexual warfare; but it can hardly be doubted that true teeth primarily had to do with the nourishment of their possessor.

The subject of the homologies of the teeth cannot be fully entered upon until the details of their development have been mastered; still, a few words may even at the outset be devoted to the elucidation of their real nature.

The mucous membrane which lines the alimentary canal is continuous with the external skin, with which it blends at the lips. Now, if a young dog-fish just about to be hatched, be examined, it will be found that it has no distinct posterior lip, but that its skin turns in over the rounded jaw without interruption. The skin outside carries spines (dermal denticles, placoid scales),* and these spines are continued over that part of it which enters the mouth and bends over the jaws, being slightly larger in this latter position.

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* "The placoid scale has the structure of dentine; is covered by enamel, and is continued at its base into a plate formed of osseous tissue." Gegenbaur's

It may occur to the reader that it is a remarkable thing that the skin and its associated structures should be found in the mouth at all, but a very easy explanation is afforded by the facts of embryology. At the stage immediately prior to the appearance of the embryo, the egg is enveloped by cells which are differentiated into two layers. In the neighbourhood where the embryo is about to appear, a third layer becomes separated off and placed between the other two. The origin of this third layer varies in different animals. In *Amphioxus*, for example, it is derived entirely from the inner layer.

The most superficial of the three layers is called the epiblast, the internal one the hypoblast, and the middle one the mesoblast.

From the epiblast are ultimately formed the enamel of the teeth, the epithelium of the mouth (with the exception of that which covers the tongue and the back part of the floor of the mouth), the lining of the anus, the skin and its appendages, hair and nails, &c., the epithelium of skin, glands, and a variety of other structures, such as the nervous system.

From the mesoblast are derived the dentine and cementum, the skeleton, and all the connective tissues of the body, the muscular system, &c., &c.

From the hypoblast are formed the epithelium of the whole alimentary canal, from the back of the mouth as far as the anus, and the other internal epithelia of various organs derived from the alimentary canal, such as the lungs, liver and pancreas.

Now, as the embryo begins to take definite shape, that part which in the future will become the intestinal tract has for some time a widely open communication on its ventral surface into the general interior cavity of the egg or yolk sac, but the embryo grows forwards and backwards in such a way as to form a blind pouch at either end, the one in front and the other behind, which are thus still in communication with the cavity of the yolk. Were this state of things to be perpetuated while the alimentary canal becomes gradually pinched off and finally closed from the yolk sac, there would be neither mouth nor anus, and the intestine would terminate in blind extremities near either end of the embryo. At the hinder end this sometimes happens, and the result is that the animal is born with an imperforate anus.

At this stage the parts are named the foregut (the blind anterior end), the hindgut (the blind posterior end), and the midgut (that portion in open communication ventrally with the yolk-sac).

The mouth is formed later by an invagination of the epiblast from the surface, so as to make a pouch (*stomodæum*) reaching down to the foregut, but it is still some time before the septum between them breaks down. The anus is formed in a similar way, the invagination (*proctodæum*) being much shallower and occurring at a later date.

Thus we have in what is to be the mouth, a portion of the actual exterior or future skin of the embryo carried in, and so it ceases to be a matter for surprise that we should find in the mouth skin structures, viz., dermal denticles.

It is, however, pointed out by Dr. Wortman (5), on the authority of Mr. Ryder, that the teeth of those fish which have teeth upon the gill arches and pharyngeal bones, lie beyond the limits of the invaginated

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"Comparative Anatomy," translated by F. Jeffery Bell, p. 424. (The term "Dermal denticle" is therefore preferable to that of "Placoid scale," since it better expresses both the structure and position of the spine.—Ed.)

integument, and are therefore of hypoblastic derivation. He goes on to add that, if this be true (which is not certain), the generalisation that all teeth are modified dermal spines would be incorrect. It might be, however, an example in which identical structures have been produced in a similar manner from tissues of different origin, and in all probability be attributable to the same cause, viz., repeated stimulation of a particular point, which eventually gave rise to a calcified papilla.

The probable explanation of the origin of many of the teeth in these positions is that they are derived from lateral invaginations of the epiblast, similar in character to the anterior *stomodæum.* These invaginations meet with lateral evaginations from the walls of the foregut. The bilaminar membrane separating the cavities of these epiblastic and hypoblastic pouches ultimately ruptures, thus giving rise to the pharyngeal gill slits, which are consequently formed in a manner comparable with that of the mouth. Likewise, the origin of the teeth upon the gill arches will be the same as of those situated in the mouth.* This explanation, however, cannot apply to all the tooth-like structures found in them and some other positions, for example, those found in the œsophagus of certain fishes (fam. *Stromatidæ*), which are situated in positions quite beyond the limits of epiblastic imaginations.

If the growth of the dog-fish be followed, those spines of the skin which cover the jaws become developed to a greater size than those outside. A groove, without spines, appears between the jaw and the lip and the identity and continuity of the two become to some extent masked. No one can doubt, either from a comparison of adult forms or from a study of the development of the parts, that the teeth of the shark correspond to the teeth of other fish, and these again to those of reptiles and mammals. It may be clearly demonstrated that the teeth of the shark are nothing more than highly developed spines of the skin, and therefore it is inferred that all teeth bear a similar relation to the skin. This is what is meant when teeth are called "dermal appendages," and are said to be perfectly distinct from the internal bony skeleton of the animal. The teeth of the shark and of many other creatures are not only developed, but always remain imbedded in tough mucous membrane, and never acquire any connection with the underlying bone. Indeed, all teeth alike are developed from a part of the mucous membrane, and any connection which they may ultimately get with the bone is a secondary matter. As has been well expressed by Dr. Harrison Allen (1), "if the hairs of the scalp were to be inserted into the skull, or of the moustache into the upper jaw, we should express great astonishment, yet such an extreme proposition is no more remarkable than what is seen to take place in the jaws ;" again, "the feathers of certain birds making impressions on the radius, the whalebone pendent from the roof of the mouth, are examples of this same association of tegumentary appendages with the bones."

To these examples may be added the horny plates of the *Ornithorhynchus*, which are pure hardenings of the stratum corneum of the oral epithelium, but nevertheless have definite beds provided for them on the bones.

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* The arrangement of the pharyngeal teeth and the degree to which they are developed vary greatly. Many of these have been described by Colonel Shepherd in a series of papers which have appeared from time to time in the *Zoologist*.—Ed.

In their simpler forms, then, teeth are met with as very numerous spines, differing but little from the spines of the skin except in size, and still less from one another. Indeed, if we take the spines of the skin where, as happens in many cartilaginous fish, some are developed to an especially large size for protective purposes, we shall often find them absolutely indistinguishable from teeth upon the jaws, so far as minute structure and general form go, though they may perhaps exceed the teeth in size.

Nickerson (³) has minutely investigated the development of the scales of *Lepidosteus*, which, at all events at an early period, carry upon them small spines. He regards these spines alone as perhaps homologous, with the scales of the shark, the whole scale of *Lepidosteus* then representing the fusion of a number of placoid scales and consisting, with the exception of these little spines, of their basal portions only. Somewhat similar conclusions have been arrived at by O. Hertwig (²) for the Ganoid scale; and by Marett Tims (⁴) for the scales of the *Gadidæ.*

In many fish, the teeth, in some cases more specialised than those of the shark, are scattered over almost every one of the numerous bones which form part of the walls of the mouth and pharynx. In the amphibia the teeth are more restricted in position, being found only upon the jaws and in connection with the vomers. In reptiles they are even more restricted, whilst in mammals they are absolutely confined to the premaxillary, maxillary, and mandibular bones. In fish and reptiles it is the exception for the teeth in different parts of the mouth to differ markedly from each other; in mammals it is the rule.

Most teeth owe their hardness to an impregnation with salts of lime: the organic matrix may, however, be of a proteoid substance, keratin, in which case the tooth is of horny consistence, and is spoken of as "cornified;" or the matrix may be, like that of bone, gelatigenous (that is to say, not gelatine, but collagen, the anhydride of gelatine which passes into gelatine after prolonged boiling), in which case the tooth is more richly impregnated with salts, and is spoken of as "calcified."

Horny teeth, so far as they have been investigated, consist of aggregations of cells of the stratum corneum of the oral epithelium, and they are penetrated on their under side by the papillæ, whose enormously exaggerated epithelial coats have built them up.

The great mass of a calcified tooth is usually made up of "dentine," which gives to it its characteristic form, and often practically constitutes the whole tooth. To this may or may not be added enamel and cementum.

[These facts are not without significance in view of the objection raised, by rigid upholders of the germ-layer theory, to the application of the term "tooth" to those tooth-like structures into the development of which the epiblast does not enter.]

The simplest teeth are hollow cones, and have no roots; they are calcifications of papillæ, and, as has already been mentioned, are sometimes practically identical in structure and form with similar spines upon the skin.

As these simple teeth are generally very numerous, it has occurred to some morphologists that multicuspid teeth have originated by the coalescence of several simple cones, each cusp thus being the representative of an original separate tooth. But there is a good deal to be said against the acceptance of such a view; the question can, however, be better discussed on a subsequent page. It will suffice to say here that it is much more probable that additional cusps arise by some process of evolution.

It is thus usual to speak of horny and calcified teeth; but the development of the former is less fully known, and appears to vary in different cases. Hence it is impossible to determine the exact relation in which they really stand to calcified teeth.

Before proceeding to consider the structure and comparative anatomy of teeth in detail, it may be well now to give a description of the human teeth, as being the more familiar.

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PART I.

CHAPTER I.

THE TEETH OF MAN.

The Parts of a Tooth.—For the purpose of description the three external parts of a tooth are distinguished by name, viz., the crown, neck, and root.

This distinction is made in describing human teeth, and is applicable to the great majority of mammalian teeth, though there are some forms in which no such differentiation of parts can be seen.

The crown is that portion which is exposed above the borders of the gum, and is in human teeth coated with enamel ; the neck is that portion which corresponds to the edge of the gum, and intervenes between the edges of the bony sockets and the edge of the enamel ; the root is that part which is enclosed within the bony socket, and is covered by cementum.

Of these it is to be remarked that the "neck," although a convenient and necessary term for descriptive purposes, marks an arbitrary division of less importance than that expressed by crown and root ; also that, although this division into three parts can be made in the case of socketed teeth of limited growth, no such distinction of parts can be made in teeth of perpetual growth.

Special names have been applied to the various surfaces of the crowns, as, owing to the curvature of the alveolar border, terms which have reference to back, front, or sides would in different parts of the mouth indicate different surfaces, and so lead to confusion.

The lips, cheeks, tongue, and the median line of the mouth, however, are not open to this objection, so the surfaces which are directed outward towards the lips, or cheeks, are called "labial," or "external," and those inwards towards the tongue "lingual," "palatal," "vestibular," or "internal." The interstitial surfaces are named "proximal" and "distal." *

Incisors.—Of these there are four in each jaw : two first and two second incisors.* Their working surfaces form wedges, or obtuse and blunt-edged chisels, calculated to divide food of moderate consistency.

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* The terms "mesial" and "distal," which are in general use clinically, are used in relation to the middle line of the mouth, but the terms "proximal" and "distal" are here suggested in reference to the articular ends of the jaws, as being more in accordance with anatomical usage.—Ed.

The First Upper Incisors.—The first incisors are very much larger than the second, and, viewed either from the back or front, taper with some regularity from the cutting edge to the root, the neck not being marked by any strong constriction. The crown of the tooth, as seen from the front, is somewhat square or, more strictly, oblong, its length being greater than its breadth.

The distal (median) side, by which it is in contact with its fellow, is a little longer than the proximal, so that the distal angle of the crown is a little lower and, as a necessary consequence, a little more acute than the proximal angle of the cutting edge. Near to its base the crown narrows rather abruptly, so that at the neck a space is left between the contiguous teeth.

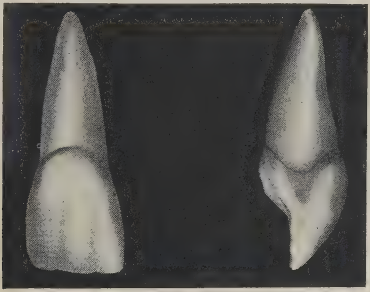

FIG. 1.—Front and side view of a left first upper incisor. A. Labial surface. B. Distal surface.† ×1½.

The *labial surface*, slightly convex in each direction, is roughly quadrilateral, and often presents two extremely shallow longitudinal depressions, which end at the cutting edge in slight notches.

In recently erupted teeth the thin cutting edge presents three slight tubercles, which soon wear down and disappear apparently by use. The edge of an incisor may be regarded as formed by the bevelling off of the dentine of the lingual surface.

The proximal and distal margins converge as they approach the boldly convex cervical border of the labial surface. Each of these two margins is slightly convex. The distal, being the longer of the two, causes the angle which it forms with the incisive border to be more acute than that formed by the proximal and incisive borders, which is frequently rounded.

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* The terms "first incisor" and "second incisor" are habitually employed to denote the human incisors from the clinical point of view, but this nomenclature is open to the objection that it is by no means certain that these teeth are the homologues of the first and second incisors of other mammals. It is also more correct to use the term "premolar" instead of "bicuspid" and "first, second and third molars" in place of "six-year old, twelve-year old, and wisdom tooth" respectively.—ED.

† The drawings of the surface views of the human teeth illustrating this chapter were made by Mr. A. W. Bell.

The *lingual surface* is nearly flat from side to side, with a slight tendency to concavity, while from above downwards it is distinctly concave and is often marked by longitudinal depressions similar to those on the labial surface. Towards the gingival margin it terminates in a distinct prominence, oftentimes amounting to a bounding ring of enamel, termed the *basal ridge*, or, in the language of comparative anatomy, the *cingulum*. It is variable in the extent of its development; it rarely rises into a central prominence at the back, but in the angle where the ridges of the two sides meet, a deep pit is sometimes left in the enamel, though this must be regarded as a departure from the normal. It is a favourite site for caries. The crown terminates on the lingual and labial aspects of the tooth in a curved line, the convexity of the curve being directed towards the gum; on both proximal and distal surfaces the curve is less regular, and its contour would be more correctly described as V-shaped, the apex of the V being towards the crown of the tooth and away from the gum.

The transverse indentations of the enamel seen both on the lingual and labial surfaces, though more especially on the latter, are marks of arrest of development, and, common as they are, are to be regarded as abnormalities.

The *distal surface* of the crown is small and triangular in shape, the apex being at the incisive angle. It is convex in both longitudinal and transverse directions.

The *proximal surface* is similar to the distal, though slightly shorter and more generally convex.

The *root* exceeds the crown in length; tapering towards its apex, it has the appearance of a triangular pyramid with rounded angles, the sides being labial, distal and proximal.

The *pulp cavity* bears a general resemblance to the external contour of the tooth. Towards the cutting edge it is very thin, and is prolonged at its two corners to a slight extent into cornua; at the neck it is cylindrical, and it is also cylindrical in the root, tapering gradually till it approaches the apex, when it becomes suddenly constricted.

The first incisors are larger than the second, though not in so great degree in man as is the case in the anthropoid apes.

Second Upper Incisors bear a general resemblance to the teeth just described but are in every dimension slightly smaller. They widen somewhat abruptly near to the cutting edge, but below this they taper fairly regularly to the end of the root. The contour of the crown is subject to wider variation than is the case of the central incisor.

The *labial surface* is convex in each direction and is widest just above the cutting edge. The proximal and distal margins converge towards the neck of the tooth, thus giving a triangular shape to this surface. The cutting edge, though somewhat more convex than in the first incisor, shows, in recently erupted teeth, the same two notches with corresponding shallow depressions running up the labial surface. Owing to the shorter length of the proximal margin the incisive edge slopes outwards and upwards.

The outer angle of the crown is far more rounded or sloped away than in the first, and the proximal surface, turned towards the canine, is in a slight degree convex. The distal surface may be slightly concave.

The enamel terminates towards the gum in contours precisely similar to those which are found in the other incisors; but the basal ridge, or cingulum, is often more strongly pronounced, and the presence of a central tubercle upon it is less infrequent. From this greater prominence of the cingulum, and consequent more marked depression in front of it, caries is more frequent upon the lingual surfaces of the upper second than upon those of the upper first incisors.

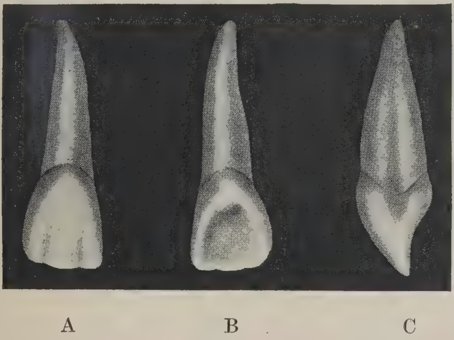


Fig. 2.—Second upper incisor (right). A. Labial surface. B. Lingual surface. C. Distal surface. ×1½.

The *root* of this tooth is laterally compressed and its apex has a tendency to curve outwards. This character often renders it possible to distinguish to which side a given tooth belongs.

The pulp cavity is, relatively to the whole tooth, perhaps a little larger than that of the first incisor; in other respects the same description will suffice.

The First Mandibular (Lower) Incisors are very much narrower than those of the upper jaw, not more than half the width at their cutting edges, which again are much wider than the necks of the teeth.

From before backwards they are broad at the neck; hence the roots are very much flattened from side to side, and rotation is inadmissible in the attempt to extract them.

The enamel contour at the neck is similar to that of the upper incisors, but there is no well-marked cingulum.

The poise of the crown upon the root is such that the distal side is in a straight line with the corresponding surface of the root; whereas the proximal side inclines outwards, thus making an angle with the root.

The *labial surface* is convex from above downwards and from side to side. The unworn cutting edge shows the three tubercles, from between which run up two shallow and inconspicuous labial grooves.

The *lingual surface* is concavo-convex, there being a marked constriction in the region of the neck causing this surface to appear triangular in shape. The two longitudinal grooves are more pronounced than on the labial surface. The enamel frequently extends further down the root on this than on the front surface of the tooth.

The root, as above stated, is laterally compressed; the surfaces converge regularly towards the apex, and each may present a median longitudinal groove, which may be more marked on the distal aspect.

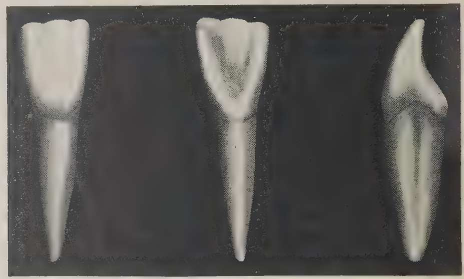


FIG. 3.—First lower incisor (right). A. Labial. B. Lingual. C. Distal views. ×1½.

The Second Mandibular Incisors, unlike the upper teeth, are distinctly larger than the first in each of their dimensions, but more especially in the length of their roots. These are much flattened, and often present on their sides a median longitudinal depression, sometimes amounting to an actual groove.

The proximal angle of the crown is rounded off like that of the upper lateral incisors, though not so markedly, and the incisive edge slopes downward towards it. The general contour of this tooth is similar to that of the first incisor, except that there is a rather greater proximal inclination of the crown upon the root, the apex of which tends also to bend in this direction. Distally, the line of the root is continued up the side of the crown as in the previously described tooth.

The Canines are in all respects larger teeth than the incisors; not only are their crowns thicker and stronger, but their roots are very much longer.

The Maxillary Canines.—The crown terminates in a blunt point, which lies in a straight line with the long axis of the root. A feebly pronounced line or ridge runs down the outer surface of the tooth from this point to the neck. The crown slopes away both before and behind the point or cusp, but as that side of the tooth which lies next to the premolar is convex, and, as it were, produced towards that tooth, the slope is longer on the proximal than on the distal half of the crown. The asymmetry of the shape of the crown makes it easy to determine at a glance to which side of the mouth the canine belongs.

The *labial surface* is roughly pentagonal and divided into a narrow distal and a broader proximal part by a feebly developed ridge running diagonally from apex to neck.

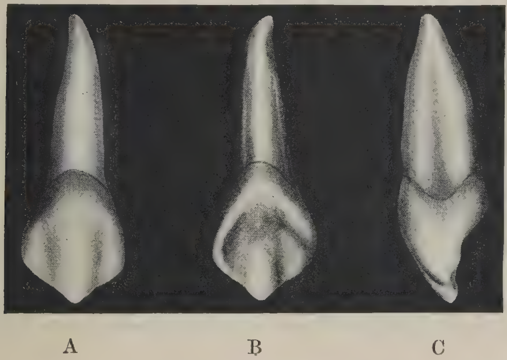


Fig. 4.—Maxillary canine (right), showing (A) labial, (B) lingual and (C) distal surfaces, the basal cusp and the three ridges which converge towards it. × 1½.

The *internal or lingual surface* is not concave like that of the incisors, but is in a slight degree convex, and a median ridge extends from the apex of the cusp ; this ridge where it meets with the ridge which borders the lingual surface and corresponds with the cingulum of the incisor teeth is often developed into a well-marked prominence or slight cusp.

In transverse section the neck is somewhat triangular, with the angles rounded, the outer or labial surface being much wider than the lingual aspect.

The Mandibular Canines are less pronounced in form than the corresponding upper teeth. The point is more blunted, the root shorter, the perpendicular labial ridge not traceable, and the want of symmetry between the distal and proximal halves of the crown less marked. Occasionally, however, the labial ridge is quite prominent, and, when present, gives to the tooth the appearance of great strength. The lingual surface has perhaps a greater tendency to concavity, and the labial surface is relatively longer, thus emphasising the slightly smaller width.

The Premolars (**Bicuspids**) are eight in number, two on each side of both upper and lower jaws, and they probably correspond to the third and fourth premolars of the typical mammalian dentition, the first and second premolars being generally regarded as unrepresented in man.

The teeth are carried round the curve of the alveolar border mainly by means of the difference in size in the external and internal portions of the canines and the two premolars.

The First Maxillary Premolar.—The crown, when examined on its occluding surface, is roughly quadrilateral, its outer or labial border being, however, larger and thicker than its inner. It has two cusps, of which the outer is the larger, stouter and broader. The two cusps are separated by a deep antero-posterior fissure. The buccal margin is surmounted about its mid-point by the external cusp, the proximal and distal slopes of which terminate at the respective angles of the crown which they help to form.

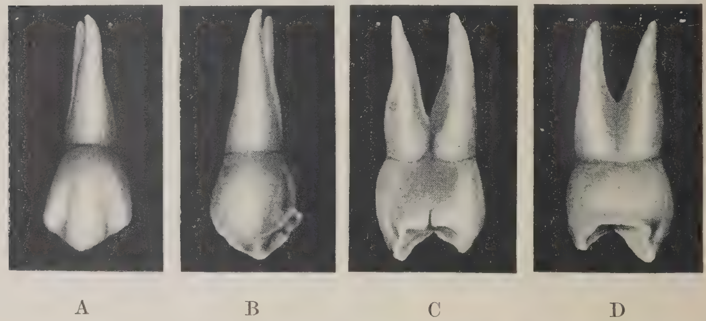


Fig. 5.—First maxillary premolar (right), showing (A) labial, (B) lingual, (C) distal, (D) proximal surfaces. ×1½.

The outer and inner surfaces (labial and lingual) are convex and smooth, with no basal ridges at the edge of the gums. It is, however, not uncommon, especially in the lower races of mankind, to see some indication of a median ridge upon the outer surface, defined by slight grooves upon either side.

The inner and outer cusps are not joined by a ridge. Instead of this there is a deep fissure, the ends of which turn somewhat abruptly outwards towards the outer aspect of the tooth. Perhaps the cingulum has been elevated to form the inner cusp, forming slight elevations bordering the anterior and posterior (distal and proximal) edges of the grinding surface. The distal surface is concave.

The root is single, and much compressed from side to side. Very frequently, however, it is double for the greater part of its length, and, if not so divided, is then marked by a groove upon each side, indicating a tendency towards such division. This tendency to division is so constant, both in the lower and higher races, that it may be regarded as almost normal. The outer border of the root is often also marked by a longitudinal furrow, which may amount to complete division. In fact, a premolar may have three perfectly distinct roots, like a molar and like the premolars of monkeys, in most of whom three is the normal number of roots. The first premolar is more variable in respect of its roots than the second.

It is thought by Topinard that in the passage from a three-rooted to a single-rooted type the postero-external root is lost, the antero-external and internal roots becoming fused.

The Second Maxillary Premolar differs from the first in that the difference in size between its outer and inner cusps is less, the inner cusp being relatively considerably larger, and indeed often preponderating over the outer cusp in length, so that the outer and lingual surfaces are nearly equal. The greater vertical convexity of the lingual surface has the tendency to bring the lingual cusp nearer to the centre of the occlusal surface than is the case in the first tooth of the series.

The distal and proximal sides of the crown are more regularly convex, and although the former is less so than the latter, it does not exhibit the depression seen in the corresponding side of the first premolar.

The *root*, usually single, is rather longer than the root of the first tooth. Longitudinal grooves may be traced on its proximal and distal surfaces. They may occasionally be sufficiently deep to divide the root into two. More frequently, if divided at all, it is only bifid in the apical quarter of its length.

The pulp cavity in the crown is furnished with distinct cornua. At the neck it is very much flattened from side to side, being often reduced to a mere fissure, which is, however, considerably larger at its two extremities than in its middle. Hence the pulp cavity of an upper premolar is difficult to fill, a difficulty increased by the impossibility, without the aid of a skiagram, of always discovering what number of roots it has, as their division sometimes takes place in varying situations.

The Mandibular Premolars are smaller teeth than those of the upper jaw, and are quite distinct in shape. The outer cusp is bent inwards, and occupies in the first premolar a position almost exactly over the apex of the root. This is correlated with the marked convexity of the labial surface of the crown. The inner cusp is very feebly developed, and is connected with the outer by a low ridge; it is also narrow, so that the tooth is somewhat triangular as looked upon from above.

The First Mandibular Premolar.—The crown is relatively more bulbous than the corresponding tooth in the upper jaw; and the lingual cusp, always small, is so diminished in some specimens as to be almost non-existent.

The root is rounded, a little larger on its outer side than on its inner, and tapers regularly towards its point. The pulp cavity is cylindrical at the neck, and also tapers regularly to the apex of the root. The cornu of the pulp which corresponds to the inner cusp is feebly developed.

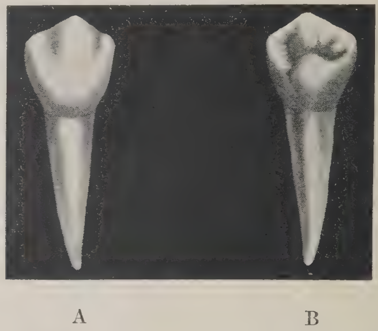


Fig. 6.—First mandibular premolar (right). A. Labial aspect. B. Lingual view, showing the preponderance of its outer over its inner cusp and the disto-lingual groove. ×1½.

The Second Mandibular Premolar differs a good deal from the first; its crown is more nearly square in shape and larger in all its dimensions. The inner cusp reaches to a higher level and is larger, and the greater development of the ridges which bound the anterior and posterior borders of the occluding surface makes it attain to such shapes as to render the tendency towards a transition from the premolar type to that of a true molar very evident.

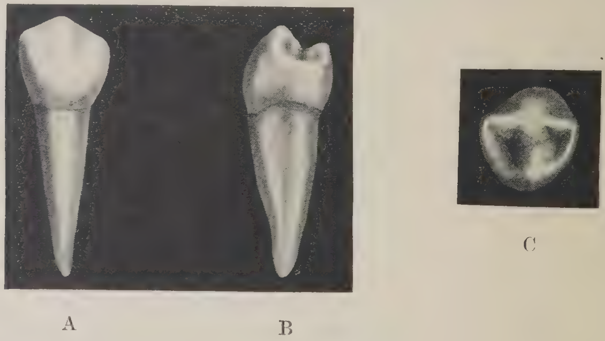


Fig. 7.—Second mandibular premolar (left), showing (A) labial, (B) proximal, and (C) occlusal views. ×1½.

The *occlusal surface*, therefore, instead of sloping obliquely in a lingual direction from the summit of the buccal cusp, as in the first premolar, is nearly horizontal. Further, by reason of the lateral development of the lingual cusp, this side of the occlusal surface is as broad as the labial side, and the outline of the surface is roughly circular rather than triangular.

The lingual cusp and the fissures which are in relation to it are subject to considerable variation, one of the most noticeable being the division of the lingual cusp into two and the formation thereby of a tricuspid tooth. In such cases the antero-posterior fissure is sharply crescentic, its horns bent outward. A deep lingual branch, emanating from a central pit, gives it a triradiate appearance.

Perhaps the more common arrangement is for the internal cusp, which is more distal in position than the external, to be joined to the latter by a ridge, thus dividing the occlusal surface into a larger proximal and a smaller distal area, a condition similar to that obtaining in the first mandibular premolar. The subsidiary cusp, which, if present, may vary in size, is developed to the proximal side of the lingual cusp. The proximal margin of the occlusal surface is longer and more convex than the distal.

The *buccal surface* resembles that of the tooth in front. The distal and proximal surfaces are markedly convex; they do not converge lingually, so that the lingual surface is as extensive as the buccal. On the other hand, they converge more rapidly towards the neck than do the buccal and lingual surfaces.

The single conical *root* is larger than that of the first premolar, and is flattened antero-posteriorly. The surface of the root is devoid of characteristic markings, but the flattened sides may have shallow longitudinal grooves. Similar longitudinal grooves may very occasionally be seen on the buccal and lingual aspects; they may even be so deep as to divide the root into distal and proximal fangs (Black).

The General Characters of the Series.—The differences between a well-developed incisor, canine, or premolar are so strongly pronounced that the resemblances which underlie them are apt to be overlooked, and it might be supposed that in shape they had little in common.

Nevertheless a very distinct gradation may be traced, and it is usual to meet with teeth which possess in a marked degree transitional characters. If the external angle of a second incisor be sloped off more than usual, while at the same time its cingulum and basal prominence be well marked, it makes no bad imitation of a diminutive canine; and such incisors are often to be met with by any who search for such deviations from the normal form.

Thus the form characteristic of a second incisor, if it be a little exaggerated, very nearly approximates to the form of a canine; indeed, in the teeth of the orang the second incisor is to all intents a diminutive canine; and in the present discussion the great comparative size of the canine, which is traceable to readily intelligible causes, may be put aside, as it tends to obscure the point to be here insisted on.

Between the canines and the premolars a similar relationship in form exists, and it is more apparent in the lower than in the upper jaw. The fact that at the base of the inner or lingual aspect of the canine may be found an elevation of the cingulum, in many instances amounting to a low cusp, has been already noted ; and it has been pointed out that the inner cusp of the first lower premolar is both smaller and lower than the other, indeed often can hardly be said to exist. A longitudinal section through the crowns of the two teeth will demonstrate without the necessity of further description that the basal cusp of the canine and the inner cusp of the premolar are the same thing, differing only in degree, while it is interesting to note that the pulp chamber in the latter has hardly any prolongation towards the small inner cusp, so that the resemblance between the two teeth is thus made more complete. Furthermore, the occlusal surface of a well-marked first maxillary premolar bears a marked resemblance to the lingual surface of an upper canine.

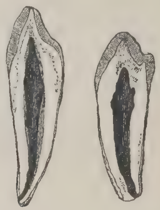


FIG. 8.—Sections of a mandibular canine and first premolar, showing the characters common to the two.

This close relationship of canines and premolars will be considered in the chapter on the homologies of the teeth ; for the present purpose it will suffice merely to point out its existence. The transition from the premolars to the molars is more abrupt ; at least, it is not so easy to point out exactly how the cusp pattern of the one would arrive at the form of the other. But it merely needs an exaggeration of the differences existing between a canine and a first premolar to make a good imitation of a second premolar.

If any one will take the trouble to make mental note of the deviations in form which he meets with in human teeth, he will find that they almost invariably consist of approaches towards the form of the teeth on either side of them ; and will infallibly be led to the conclusion that incisors, canines, and premolars are not three patterns of teeth perfectly distinct, and each *sui generis*, but that they are modifications of one and the same pattern.

The Maxillary Molar teeth have quadrilateral crowns, the angles being much rounded off. It may be premised that the first molar is more constant in shape than the second (it was regular in 99 per cent. of skulls examined), and this latter than the third.

The masticating surface carries at the corners of the quadrilateral four subequal cusps, two labial or external and two lingual or internal; the antero-internal cusp is distinctly the largest, and it is connected with the postero-external cusp by a thick oblique ridge of enamel, the remaining two cusps having no such connection.

This oblique ridge on the upper molars is met with in man, the anthropoid apes, and certain new-world monkeys.

The grooves which separate the cusps pass down on to the labial and lingual surfaces of the crown, but are lost before reaching the gum. At the place where they terminate, however, there is often a pit, which is a very favourite situation for caries, especially on the outer aspect of the teeth. It is very rare to see the grooves passing down upon the proximal or distal surfaces of the crown, a raised border of enamel generally cutting them short in this direction.

When one cusp is suppressed, it is always the postero-internal.x

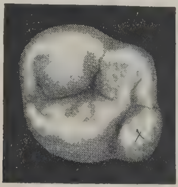


FIG. 9.—Masticating surface of a first maxillary molar on the left side; the oblique ridge connects the antero-internal with the postero-external cusp. ×1½.

The roots are three in number, two external or buccal and one internal or palatal. The latter is the largest, and runs in a direction more strongly divergent from the axis of the crown than the other roots. It is directed obliquely inwards towards the roof of the palate, is subcylindrical, and often curved.

The external roots are less cylindrical, being mutually compressed, so that their largest diameter is transverse to the dental arch; the anterior is rather the larger of the two and is more strongly pronounced on the side of the neck of the root. The antero-external root is occasionally confluent with the palatine root, but still more frequently the posterior buccal and palatine roots are confluent. Occasionally, also, four distinct roots may be met with.

The First Maxillary Molar presents an occluding surface which is rhombic in outline, the antero-external and the postero-internal corners forming the acute angles of the figure; the "oblique ridge" dividing it into two triangles forms the shorter diagonal. Each triangle contains a fossa from which the two main fissures of the crown take origin. The anterior fissure separates the buccal cusps, and may be traced on to the buccal surface, upon which it extends about half-way up the crown. The posterior fissure divides the lingual cusps. The oblique ridge is less elevated than the cusps, and is crossed by a shallow groove which joins the two fossæ. The anterior and posterior marginal ridges are sharply defined, becoming confluent at their extremities with the respective buccal and lingual cusps. Owing to the greater convexity of the lingual surface of the upper molars, the cusps on this side appear to be carried nearer to the mid-antero-posterior axis of the tooth than are the buccal cusps. In the lower molars the reverse condition holds good. A fifth cusp is sometimes present on the first maxillary molar, but is not seen on the other two. When present it is applied to the lingual side of the antero-internal cone, from which it is separated by a horseshoe-shaped fissure. When it occurs, it is usually bilateral, and is said to be inherited.

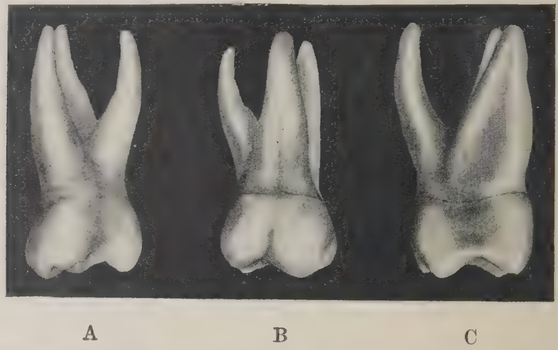


FIG. 10.—First maxillary molar (left), showing (A) buccal, (B) lingual, and (C) distal surfaces. × 1½.

The *buccal surface* is convex in each direction, and by the rapid divergence of its sides from above downwards it is wider near to the occlusal edge than at the cervical margin. The proximal border is more definitely convex than is the distal. The buccal fissure, as has been mentioned, is a continuation on to this surface of the anterior fissure of the occlusal surface, and frequently terminates in a pit. More rarely it can be traced to the bifurcation of the roots.

The *lingual surface* is similar to the buccal, except that, as it terminates in the single palatal root, it is more constricted at the gum margin, and both distal and proximal borders are convex. The cutting edge is surmounted by the two lingual cusps, of which the anterior is the larger. The deep lingual groove which makes its appearance between these two cusps not only divides the enamel surface into two distinct lobes, but is often continued as a longitudinal depression up the lingual aspect of the palatal root. The fissure which lies in the bottom of this groove usually terminates in a pit half-way between the occlusal and cervical margins, but, when a fifth cusp is present, the pit receives also the lingual extremity of the fissure which surrounds it.

The *distal surface* is nearly flat, and, since it is carried well down to the antero-buccal cusp, it forms with the buccal surface the prominent antero-external angle of the crown. On the palatal aspect, however, owing to the greater convexity of the lingual surface, it is rounded off and, without forming a prominent angle, it becomes continuous with the lingual surface.

The occlusal border, formed by the antero-marginal ridge which joins the two anterior cusps, is concave ; and the cervical margin is straight or very slightly concave towards the root. Towards this margin the surface frequently presents a broad depression which extends upward on to the antero-buccal root.

The *proximal surface* is very similar, except that the postero-external angle which it forms with the buccal surface is obtuse rather than acute. It is convex in each direction, but near the cervical margin, to the buccal side, there is a marked depression which is continued upwards on to the flattened proximal surface of the postero-buccal root.

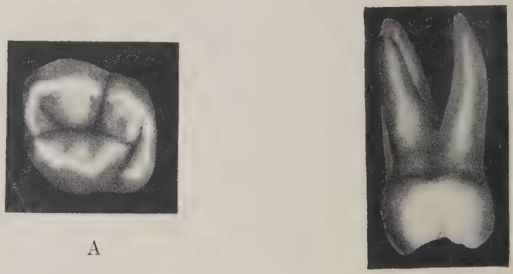
The *root* usually presents three distinct and separate fangs : two external, or buccal, and one internal, or palatal. It is noticeable, however, that division does not take place immediately below the crown, as in the temporary premolars, but that the fangs are attached to the crown by an undivided portion which may extend a full third of the total length of the root.

The palatal root is the largest, and takes a direction more strongly divergent from the axis of the crown than the other two. It is directed obliquely inwards towards the mid-line of the palate, but in its apical half or third often curves outward again towards the external roots. In shape it is subcylindrical and tapers in young normal specimens to a pointed apex. The external roots are less cylindrical, being mutually compressed so that their largest diameter is transverse to the line of the dental arch. The anterior is the larger of the two, and is the more pronounced at the neck, where its outer border becomes continuous with the prominent antero-external corner of the crown. The shallow depression seen on the distal surface of the crown is often continued upon the flat anterior surface of this root throughout its length, and it may be that penetration through gives rise to the accessory root, which, when present, is usually situated between the antero-buccal and the palatal. The root tapers at the expense of its lingual rather than its buccal edge, and displays a marked proximal inclination towards the apex.

The posterior buccal root is the smallest of the three, but bears a general resemblance to the anterior fang. It is much less prominent at the neck than the anterior, but its buccal divergence is usually greater. When viewed from the outer side it is sometimes straight, but more frequently it is curved either towards the anterior root or in a proximal direction away from it.

The Second Maxillary Molar is usually somewhat smaller than the first and, in its normal form, so closely resembles it that a detailed description is unnecessary. It is, however, subject to greater variation.

The postero-internal cusp is relatively smaller, and a fifth lobe is not found. The variations range from slight distortion of the fissures to a complete change of tooth-form. For example, the posterior fissure of the occlusal surface may be represented merely by a pit in the distal fossa, in which case the marginal ridge forms a continuous wall around the fossa from the antero-internal cusp to the posterior marginal ridge. Or, on the other hand, of the gross variations to which this tooth is subject, one of the most constant is the occurrence of the "oblique-rooted" molar. The whole tooth is compressed antero-posteriorly, and the postero-external root with that portion of the crown which it carries is displaced forwards and inwards between the antero-external and the internal fangs. In extreme cases the three roots may be in a straight line transversely; the occlusal surface of the crown then appears as an elongated oval ring of enamel enclosing a median fissure, the sides of which may be deeply and irregularly puckered.


A

B

Fig. 11.—Second maxillary molar (left). A. Occlusal surface. B. Proximal surface. ×1½.

In such a tooth the distal surface may present a broad shallow concavity, whilst the proximal aspect is convex.

The roots are smaller than those of the first molar, the internal (palatal) being less divergent. All three frequently show a distinct inclination of their apices proximally and a marked tendency to coalesce.

If two roots only are confluent, they are the internal with one of the external roots, more frequently the posterior. In some cases, however, all the roots are fused.

The Third Maxillary Molar of the upper jaw resembles in a general way the first and second, that is, when it is well developed and placed in a roomy dental arch. But amongst most civilised races it may almost be said to be exceptional for these teeth to be regular either in form or position, so that extreme variability prevails among them.

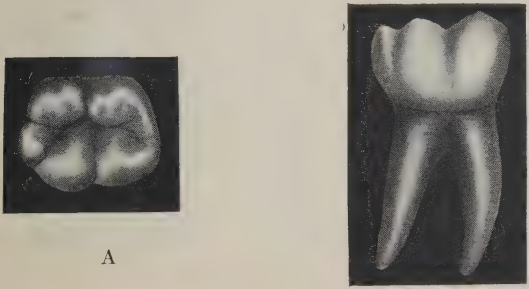
The two inner tubercles are often blended together, and the roots confluent, forming an abruptly tapering cone, the apex of which is often bent and crooked, so that but little vestige of the three roots can be traced, the pulp cavity even being quite single.

The Mandibular Molars.—**The first lower molar** is the most constant in form, and is somewhat the largest.

Its *occlusal surface* is trapezoid in shape, and presents five cusps.

Four cusps are placed regularly at the angles of a square, these being divided from one another by a cruciform fissure.

The antero-posterior diameter of the occlusal surface is greater than the transverse, and its buccal margin is the longest and has a slight outward convexity. The other three margins are almost straight. The fissures are deep and clearly defined, the point of intersection being marked by a pit which lies to the lingual side of the mid-occlusal point. The anterior limb of the crucial fissure separates the antero-external from the antero-internal cusp, and terminates either in a shallow pit or by bifurcating just short of the distal margin. The posterior arm of the crucial fissure bifurcates, and between its diverging arms is the fifth cusp, which may occupy the median line of the tooth, but more often is somewhat to the outer side. It is distinctly visible when viewed from the labial aspect. The outer limb of the bifurcation passes over the proximal margin, and, owing to the outward displacement of the fifth cusp, this limb of the fissure appears on the buccal surface of the crown. The transverse fissure passes over the limits of the occluding surface, and on the outer surface of the tooth may end in a pit, which is a common site for caries; although it occasionally passes over the



A

B

FIG. 12.—Occluding and external surfaces of a first right mandibular molar. × 1½.

lingual surface, it is here less pronounced. Of the external cusps the anterior is the highest, and usually occupies more than a third of the buccal margin. The anterior lingual cusp is also usually higher than the posterior. It should be noted that, owing to the long vertical convexity of the buccal side, the cusps which surmount it are carried towards the mid-antero-posterior line of the occlusal surface, whereas the lingual cusps rise vertically from the lingual side. This condition is the reverse of that which obtains in the corresponding upper tooth.

The *buccal surface*, quadrilateral in shape, is interrupted by the two fissures just mentioned, thus dividing the surface into three convex areas. Near the cervical margin, a horizontal ridge of enamel, the "bucco-cervical ridge," is frequently seen in this, as in the other molars.

The *lingual surface*, convex in every direction, is more perpendicular than the buccal, and since it forms a segment of the inner arc of the dental arch, it is much narrower.

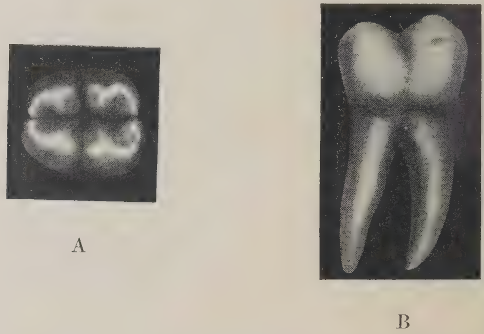


FIG. 13.—Occluding and external surfaces of second right mandibular molar. ×1½.

The *distal surface* frequently shows a concavity extending upwards from the roots.

The *proximal surface* varies in accordance with the relative position of the fifth cusp, as mentioned above. The first lower molar had five cusps in 82 per cent. of all skulls examined.

Lower molars are implanted by two roots, placed anteriorly and posteriorly; the roots are much flattened from before backwards, and they are very usually curved slightly backwards. In the median line of each root there is usually a groove, by the deepening of which four roots may be produced; or this may happen with one root only, more frequently the anterior, so that a three-rooted tooth is the result. While these characteristics apply to the roots of all the mandibular molars, the peculiar characteristic of the root of the first tooth of the series is that the fangs diverge at their origins, but nearer the apices bend towards one another, the axis of the anterior being greater than that of the posterior.

The Second Mandibular Molar does not greatly differ from the first, save that the roots are more often confluent, and the fifth cusp less marked, even if it exists at all. It is present in about 24 per cent. of skulls.

The Third Mandibular Molar is subject to greater variation of form than any tooth of the series. It is seldom so small as the corresponding upper tooth, and its crown is often large even when its roots are very stunted. It has five cusps, as a rule, and bears a more or less close resemblance to the molars which precede it, but very frequently it differs widely from either of these, and in larger specimens may present a confusion of fissures and cusps. It is either two-rooted, or, if the roots be confluent, a groove usually marks a tendency to a division into two fangs. Three fangs are not infrequent, and when present are usually short and irregular. The roots are comparatively shorter than the other molars, and are directed more acutely backwards.

It is stated by Professor Owen (3) that, although the third molar is the smallest of the series, the difference is less marked in the Melanesian than in the Caucasian races, adding also that the triple implantation of the upper and the double implantation of the lower is constant in the former races. More extended observations have overthrown this statement as a positive dictum to be accepted without exceptions, but it may nevertheless be taken as expressing a general truth.

In lower molars the inner, and in the upper the outer, cusps are the longer.

The Deciduous Teeth.—The milk teeth differ from their permanent successors by being smaller and having more bulbous crowns, so that the neck is more strongly constricted. The enamel is distinctly whiter than that of the permanent teeth. The incisors and canines are somewhat similar to their successors, the canines, however, being relatively shorter and broader than their representatives in the permanent dentition.

The deciduous premolars are quite unlike their successional teeth, but the second temporary premolar, both upper and lower, bears a striking resemblance to the corresponding first molars of the permanent series.

The chief difference in form between the deciduous upper central incisor and its successor is that the distal and proximal sides of the crown are more convex, a condition which is particularly marked on the latter side. The root is relatively longer than that of the permanent tooth, and frequently exhibits in its apical fourth a distal, and sometimes a labial, inclination.

The deciduous upper lateral incisor is similar to the central incisor, except that, like its permanent successor, it is a narrower tooth, and, as the distal side also tends to greater convexity, both angles are more rounded. In length it is equal to, and may even exceed, that of its neighbour.

The lower incisors are practically miniatures of their successors, and, as in the latter, the lateral incisor is rather larger than the central. In the deciduous lateral, however, the proximal angle of the crown is often rounded, and the tooth then approximates both in form and in size to the corresponding milk tooth in the upper jaw.

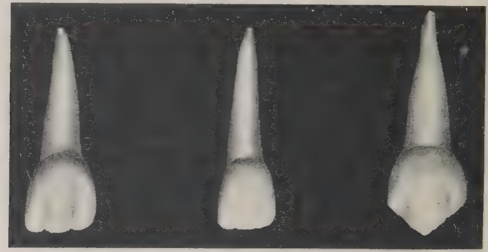


FIG. 14.—Deciduous upper central and lateral incisors, and canine (left), labial aspect. × 1½.

Except for the features common to the deciduous series and the relative shortness of the upper tooth, the milk canines, both upper and lower, do not differ widely from their successors. The length of the incisive edge in the upper tooth is relatively longer, and the lateral angles, owing to the bulbous nature of the crown, though well rounded, are more prominent.

The deciduous premolars differ so widely from the permanent teeth as to necessitate a separate description of each tooth. They all have the characteristic enamel of milk teeth. They are constricted at the neck, and this feature is exaggerated by the wide divergence of their fangs, which in each case are spread to embrace the crown of the permanent successor. Like the permanent premolars, the upper teeth are three-rooted, and the lower ones two-rooted.

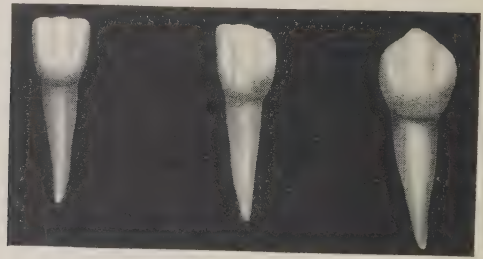


FIG. 15.—Deciduous lower central and lateral incisors, and canine (left), labial aspect. × 1½.

The First Deciduous Upper Premolar may be regarded as tricuspid and presents an occlusal surface which is roughly triangular, the base being formed by the external marginal ridge, and the apex by the summit of the lingual cusp. The buccal margin is almost straight, and in unworn specimens shows an anterior and posterior cusp separated by a shallow groove. These elevations, however, are frequently lost early, and the tooth then exhibits a moderately sharp unbroken ridge of enamel, which is joined at its extremities by the low distal and proximal marginal ridges to the corresponding slopes of the prominent lingual cusp.

The occlusal surface is divided by a median antero-posterior fissure, which usually terminates at each end in a bifurcation. The buccal limb of the anterior bifurcation frequently ends in a pit situated in the angle formed by the buccal and the anterior marginal ridges, the lingual limb continuing in the line of the main fissure. A deep pit marks the point of bifurcation of the main antero-posterior fissure at its hinder end, and the diverging limbs, which are short, do not indent the posterior marginal ridge, but lie parallel to it. From the buccal limb a shallow groove passes over on to the buccal surface, and forms the division between the buccal cusps, of which the anterior is the larger.

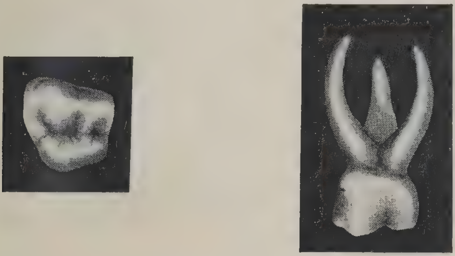


FIG. 16.—Occluding and external surfaces of first deciduous upper premolar (left). × 1½.

The free margin of the external ridge and the apex of the lingual cusp incline towards each other, with the result that, viewed from above, the prominent bulges of the buccal and lingual surfaces of the crown are very noticeable, and give to the tooth a characteristic appearance.

Sometimes a fourth cusp is present, in which case it is situated postero-internally, and is a small cusp applied, as it were, to the posterior aspect of the lingual cusp, from which it is separated by a horseshoe-shaped fissure.

The buccal surface is quadrilateral, and is wider at its cutting edge than at the constricted neck. It is flattened, and towards the cervical margin there is a prominent ridge of enamel, which is more pronounced over the anterior root.

The lingual surface is composed of the "globular" lingual cusp which surmounts the internal (palatal) root, and is markedly convex in every direction.

The proximal and distal surfaces are almost flat from side to side, but, whereas from above downwards the latter becomes concave towards the root, the former is uniformly convex.

The roots are placed similarly to those of the upper first permanent molar, but are very divergent and flattened, the external ones antero-posteriorly and the internal transversely.

The Second Deciduous Upper Premolar is intermediate in size between the preceding tooth and the first permanent molar, to which it bears a remarkable resemblance. It is usually a quadricuspid tooth, and although bulbous in the crown, and prominent like the permanent molars over the antero-external root, it does not present the buccal bulge typical of the first deciduous premolar. As in the case of the first permanent molar, quinquecuspid specimens are not uncommon, in which case the extra cusp is developed on the side of the antero-internal cusp, which is then displaced towards the middle of the occlusal surface, and the distal side may be increased to twice the width of the proximal.

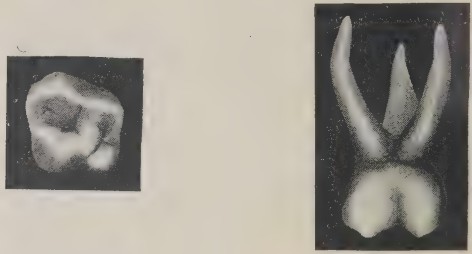


Fig. 17.—Occluding and external surfaces of second deciduous upper premolar (left). × 1½.

The roots are flattened, as in the first deciduous premolar, and are widely spread, but exhibit a tendency to convergence at their apices, which is particularly marked in the buccal fangs.

The First Deciduous Lower Premolar is quadricuspid; its occlusal surface is quadrilateral, the longer diameter being in the antero-posterior direction. The buccal and lingual sides are almost parallel, and the antero-external angle is prolonged acutely forwards. Of the cusps the two internal are higher than the two external. The margins are sharply defined, and a ridge of enamel connects the antero-external with the antero-internal cusps, thus dividing the surface. This ridge separates two fossæ, a larger posterior and a smaller anterior.

The buccal surface is flattened and quadrilateral, and, as in the corresponding upper molar, presents a marked buccal ridge of enamel, terminating anteriorly in a distinct prominence, which dips down upon the anterior root.

The lingual surface is uniformly convex from above downwards, slightly so from side to side, and is usually devoid of markings. The proximal and distal surfaces are slightly convex in each direction, the former being less irregular in shape.

The roots are very flattened antero-posteriorly and widely divergent, and both exhibit median longitudinal grooving, which is particularly marked in the anterior fang.

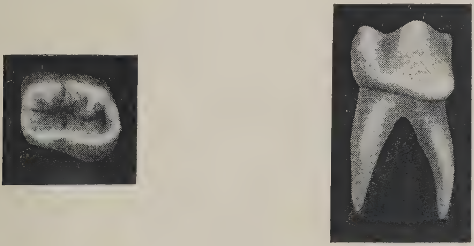


Fig. 18.—Occluding and external surfaces of first deciduous lower premolar (right). × 1½.

The Second Deciduous Lower Premolar so closely resembles the first permanent molar in the arrangement of its cusps and the conformation of its fissures that a detailed description is unnecessary. It has five cusps: two external, two internal, and a small cusp placed between the postero-internal and postero-external cusps. In the size of its occlusal surface this tooth is often but little smaller than its permanent neighbour. It differs from the latter, however, in displaying to a marked degree the characteristics of deciduous teeth previously described, namely, the white enamel, the constricted neck, and the flattened, widely divergent roots. There is no buccal prominence of enamel, as is seen in the deciduous first molars.

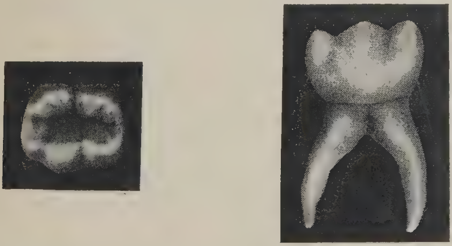


Fig. 19.—Occluding and external surfaces of second deciduous lower premolar (right). × 1½.

The Dental Formula of Man.—In viewing the gradational characters which exist between the various human teeth, it must not be forgotten that some links in the chain have dropped out.

The typical number of teeth in existing mammals may be regarded as 44, *i.e.*,

$$\mathrm{i}\,\frac{3}{3}\;\mathrm{c}\,\frac{1}{1}\;\mathrm{pm}\,\frac{4}{4}\;\mathrm{m}\,\frac{3}{3} = 44,$$

whereas man has only

$$\mathrm{i}\,\frac{2}{2}\;\mathrm{c}\,\frac{1}{1}\;\mathrm{pm}\,\frac{2}{2}\;\mathrm{m}\,\frac{3}{3} = 32.$$

It has been usual to suppose that the teeth which are missing in man are the third incisor on each side and the first and second premolars, but reasons have been advanced which throw doubt upon this conclusion as regards the incisors (^{2}, ^{6}). From the study of cases of cleft palate it has been found that it is not at all certain that the cleft usually runs along the site of the suture between the premaxillary bone and the maxilla; for it often appears to be well within the limits of the former, and so lends some support to the idea of Albrecht (^{1}) that there are two intermaxillary bones on each side,* and that the cleft runs along the division between them. And it is far from uncommon for a tooth of incisor type to lie beyond the cleft and close against the front of the canine. To this tooth Sir W. Turner (^{5}), pending decision as to its homologies, gives the name of "precanine." The argument put briefly is this: a tooth outside the cleft and close to the canine is of so common occurrence that its position there must be due to something other than accident when the normal number of incisors is not exceeded. But there is a case on record in which this precanine existed although there were four incisors upon the intermaxillary portion, which was isolated by a double cleft; in this specimen, therefore, the precanine was evidently the third incisor of the normal mammalian dentition, and it is therefore not unlikely that it is always so; if this inference be correct, then the lost incisor in man is probably the second.

The Arrangement of the Teeth in the Dental Arches.—The teeth of the upper jaw are ranged along a curve of larger dimensions than those of the lower, the incisors passing in front of the corresponding lower teeth, and the external cusps of the premolars and molars closing outside those of the lower teeth.

There are, however, some points to be noted in the relation borne by the upper to the lower teeth, by which it is brought about that each tooth is antagonised by portions of two teeth in the other jaw, and has therefore not merely a single opponent.

The upper incisors and canines when the mouth is closed, from the larger size of the arch in which they are arranged, shut over and in front of the lower teeth, concealing the upper thirds of their crowns; while the external tubercles, or cusps, of the premolars and molars of the lower jaw are received into the depressions between the external and internal tubercles of the similar teeth in the upper jaw, thus allowing the external tubercles of the upper teeth to close externally to the outer tubercles of the lower row.

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* Comparative anatomy, however, lends no support to this view.

Beyond the incisors, each lower tooth closes somewhat in front of its corresponding upper tooth.

In consequence of this arrangement of the tubercles, the whole surfaces of the crowns of the opposing teeth are used during mastication, this act being performed by bringing the external tubercles of the lower molars opposite to those of the upper row, whence, by the lateral motion of the mandible inwards, their external tubercles pass down the inclined surfaces of the external and up those of the internal tubercles of the upper teeth, crushing in this action any interposed substance.

It will also be observed that, from the difference of width in the incisors of the two jaws, the first incisors of the upper extend over the first and half of the seconds of the mandibular series, and that the superior seconds lie over the remaining half of the inferior seconds and the anterior half of the canines of the lower jaw. The upper canines close over the halves of the lower canines and first premolars, while the first premolars impinge on the half of the first and half of the second premolars of the lower row. The second upper premolars close upon the anterior third of the opposing lower first molars and the posterior halves of the second premolars.

The upper first molars occlude with the posterior two-thirds of the first and one-third of the second molars of the lower jaw, while the second upper molars close upon the unoccupied posterior third of the second and the anterior third of the third molars. The maxillary third molar being smaller in size than that of the lower jaw, is opposed perfectly by that portion of the latter left unoccupied by the second mandibular molar.

By this admirable arrangement no two teeth oppose each other only, but each tooth in closure of the jaw impinges upon two, so that should a tooth be lost, or even two alternate teeth, still the corresponding teeth of the opposite jaw are opposed to some extent, and thus remain useful. For when a tooth is wholly unopposed a process is apt to be set up in the jaw by which the useless organ is gradually ejected.

The direction of the teeth in the upper jaw is vertically downwards and slightly forwards, while those of the mandible are placed vertically, the molars tending slightly inwards.

It should be borne in mind that the description of the human teeth here given is that which may be regarded as typical for the European races of to-day. The teeth of other human races as well as of those of earlier and of prehistoric times exhibit certain points of difference. These will, however, be considered in a later chapter, in which the dentitions of the Primates are dealt with from the comparative point of view.

THE FACIAL AND MAXILLARY BONES.

Without dwelling upon details which are to be found in every anatomical text-book, there are some considerations of especial interest to the odontologist which are often passed with little notice. Thus the close interdependence between the dentition and the general appearance of the face, and, indeed, even the shape of the skull as a secondary result, is apt to be forgotten.

Thus, to take a lion as an example, the snout is broad, owing to the wide separation between the canines, which gives these teeth a good purchase in grasping a living prey. Its shortness enables them to be used at a greater mechanical advantage than would be the case were they further removed from their fulcrum at the joint, and the breadth of the face below the eyes is conferred by the widely spreading zygomatic arches, which are obliged to be wide to give passage to the very powerful temporal, and attachment to the masseter muscles.

The size and strength of the muscles are correlated with a lateral compression of the cranial portion of the skull, together with the development of bony ridges to form additional surface for the origin and attachment of muscles acting upon the mandible, thus largely influencing the contour of the face.

Such a skull is in marked contrast with the long thin snouts of the Insectivora, whose forceps-like front teeth, as a rule, merely pick up unresisting prey; or with the long weak snouts of the horse and the Ungulata generally. The face of the boar, again, is largely determined by the great muscles which move the jaw, and by the bony processes which give attachment to them.

The adult anthropoid ape has a shorter face, associated with a dentition with closely-packed teeth, not very divergent in shape from the human type, but he remains prognathous, and with a face that is disproportionately large as compared with his cranium, because he has teeth that are relatively larger and more powerful than those of man, and he has a diastema between them to admit his great canines. In the young ape, however, with a less powerful dentition, the contrast with man is much less marked.

Or, if the human face be taken as an example, and the jaws be extended forward a little, the teeth projected and the mouth widened, a coarse animal type of face is copied; and, conversely, by a reduction of the maxillary region, perhaps even below the limits which will afford space for the regular disposition of the teeth, a refined oval type of face is formed, such as is represented in many of the ancient Greek sculptures.

The jaws of a negro are large relatively to the cranium, as are also those of exceptionally big men, though this is not universally true. In rickets the jaws are disproportionately small.

The motions executed in mastication, as well as the crown-patterns of the individual teeth, differ much according to the nature of the food. Hence it happens that in different animals the muscles of mastication and the type of tooth-pattern are very variously developed.

Thus in the herbivora there is great lateral movement of the jaw, as any one may observe, while the pterygoid muscles, and especially the external pterygoid, attain to a very large relative size.

On the other hand, in the rodents, which move their jaws backward and forward in gnawing, the masseter muscle is enormously developed, and has a very marked general backward direction.

Although it is not strictly true, the masseter and temporal muscles may be said to be developed in mammals in an inverse ratio to one another: when one is large the other is small. But though the former is at a maximum in the Carnivora, in which little lateral movement of the jaws is possible, the latter is highly developed in many of the class.

In the great apes, the temporal muscle becomes enormously developed only at the period of second dentition; this fact, conjoined with its size, which in ungulates seems to have some relation to the presence or absence of canines, would incline one to suppose that it is useful in that rapid closure of the mouth appropriate to the seizure of prey or to fighting.

It may be noticed that, whilst the powerful (masseter, temporal, and internal pterygoid) muscles close the jaws, only slight and weak ones (digastric, mylohyoid, and geniohyoid, aided perhaps by the platysma) open them, and the weight of the mandible is enough *per se* to open the mouth.

The position of repose is neither complete closure nor opening of the jaws; in persons with nasal obstruction the habitual position is one with the mouth somewhat more widely open, owing to the difficulty of breathing through the nose, a fact which may cause an irregularity in the disposition of the teeth.

Just as the muscles of mastication vary in their relative development in accordance with the food to be dealt with, so also do the salivary glands.

As a rule herbivorous creatures have large parotid glands; that is to say, those creatures which deal with the driest food and masticate it the most have this gland largely developed. For instance, it is very large in the ox and other ruminants; in herbivorous marsupials it is larger, and in the carnivorous section smaller, than the submaxillary gland. When an especially viscid fluid is required, as, for example, that which lubricates the tongue of an ant-eater, it is furnished by exceedingly large submaxillary glands.

The form of the glenoid cavity also bears an intimate relation to the type of dentition of the animal and the nature and extent of the movement of its jaws.

Thus in a child it is nearly flat, with no well-marked surrounding elevations ; its axis is transverse, and little rotary motion is made use of. In the adult it is deeply sunk ; the axis of the condyle is oblique, and rotary movements are largely made use of in triturating food.

In the *Felidæ*, it is strictly transverse ; their teeth, adapted for slicing but not grinding, would gain nothing by lateral motion, which is rendered quite impossible by the manner in which the long transverse condyles are locked into the glenoid cavity by strong processes in front and behind. Curiously enough, the interarticular cartilage is present, but as the condyle never moves forward, the cartilage is not attached to the external pterygoid muscle.

In the Ungulata the condyle is rounded, the ascending ramus long, the pterygoid muscles large, and the glenoid cavity shallow. In the whale, which of course does not masticate at all, there is no interarticular cartilage and no synovial membrane ; the articulation is reduced to a mere ligamentous attachment.

In rodents there is no postglenoid process, so that the condyles have a large play backwards, useful for employing the teeth in gnawing.

The articulation of the human lower jaw is peculiar, and allows of a degree of play quite unusual in a joint. The ovoid condyles when the jaw is at rest are lodged in depressions, the *glenoid fossæ* of the temporal bones, formed partly by the squamous and partly by the vaginal portions of the bone. In the anterior-posterior direction the fossa is much larger than the condyle which rests upon its anterior portion ; the posterior half of the cavity is rough, and lodges a portion of the parotid gland ; the anterior is smooth, and is bounded in front by the *eminentia articularis*, which is the middle root of the zygoma, enters into the formation of the joint, and is coated over by cartilage even beyond its summit. Between the condyle of the lower jaw and the temporal bone lies a movable *interarticular fibro-cartilage*, which is an irregular bi-concave oval plate, the edges of which are united with the capsular ligament, so that the joint is divided into two cavities, furnished with separate synovial membranes, unless when, as sometimes is the case, the fibro-cartilage is perforated in its centre. It is thickened at its posterior border, which lies in the hollow of the glenoid fossa. Above it the bone is thin, the dura mater being close at hand, and it may be useful in deadening shocks. The startling effect of a " knock-out " blow is due to shock transmitted through the condyle.

The lower surface of the cartilage is concave, and, as it moves forward with the condyle in its excursions, it provides the latter with a concave seating in which to revolve in all positions of the mandible, for it is more closely attached to the condyle than to the skull.

An interarticular fibro-cartilage is constant in, and peculiar to, the Mammalia.

The exact nature of the movement of the mandible in opening and closing the mouth was studied by John Hunter, and more recently by other observers, especially with regard to the results produced by the laxity of the articulation and the consequent latitude of movement allowed to the condyle. In the *Felidæ* the glenoid cavity is so complete and fits with such accuracy the form of the condyle (an interarticular cartilage being, however, interposed), that only a pure hinge motion is possible, and consequently any part of the mandible must, in the opening of the mouth, describe an arc of a single circle having for its centre the condyle. In any animal, however, in which the condyle is free to move forwards, this will only be true so long as the condyle remains stationary, in other words, so long as the centre round which the arc is described remains in the same place. It was formerly supposed that during the opening of the mouth to a small or moderate extent the condyle did, in man, remain in the same position, and that it was only when the opening was somewhat extreme that it passed forward and on to the *eminentia articularis*. It has, however, now been demonstrated, first by Dr. Luce and subsequently, by other methods, by Mr. Dolamore and the author (⁴), that this is not the case, but that the condyle commences to travel forwards from the first. Its motion of translation is not equal for equal increments in the opening of the mouth, being at first less, then increasing in the middle of its course, and finally, as the condyle has mounted the eminence, again diminishing. It becomes then obvious that the path described by a point in the mandible, say by the mandibular incisors, cannot be a portion of any one circle, but would be more nearly represented by successive short segments, each described from a more advanced centre. In man, however, the sliding motion of the condyle is not,

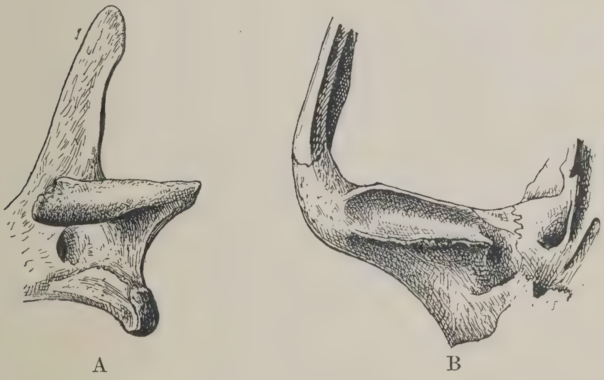

Fig. 20.—Condyle of the lower jaw A and glenoid fossa B of a tiger.

as in some creatures, simply forwards: its track is determined by the form of the surface of the glenoid cavity, so that, as it slides along, it travels along a curve the concavity of which looks forwards and upwards.

The resultant then, the path described by the mandible, is compounded of two circular motions, just like the path of a geometric cutter or a geometric chuck; in other words, the rotation of the mandible upon its condyle as a centre is complicated in its ultimate results by this centre, the condyle itself, all the time travelling along a short curved path, namely the under-surface of the glenoid fossa and the *eminentia articularis.* But this last-mentioned path, though considerably curved, is a short one, and so the resultant motion of the mandible does not depart from the arc of a circle to any very wide extent. It is obvious that the shape of the glenoid fossa and of the eminence will affect the result, and without entering into details, for which the reader is referred to the papers themselves, it may be briefly stated that the effect of this combination of movements is to carry the mandible further forwards than it would otherwise go, and to approximate its motion more nearly to a straight line;—that is to say, to make it travel almost upon the arc of a circle larger than that which would be traced by its rotation round its own condyle. It may be that this more forward path is an advantage to an animal which carries its head more or less at right angles to its neck; an animal, such as a lion or a dog, which carries its head horizontally, has plenty of room to open the mouth widely without touching its neck, whereas in man or in a higher ape the wide opening of the mandible, if it were not at the same time carried forward, would make pressure on the anterior structures of the neck. Be that as it may, it will be obvious that no simple circular motion round any fixed centre can truly represent the path of the mandible; nevertheless the actual path does not greatly diverge from the arc of a circle described round a point generally an inch or an inch and a half below the condyle, and somewhat behind it. Thus the old statement that the axis of rotation lay upon the plane of the masticating surfaces of the teeth prolonged backwards is not accurate, but is not very far from the truth.

A curious point which came out in the progress of the inquiry is that the track pursued in opening the mouth, as shown by tracings, is not identical with that pursued in closure, the latter generally lying in front of the former and only becoming coincident at the last moment, just before the teeth meet.

When the mouth is forcibly closed the lower teeth only are moved; the upper teeth have to be rigidly fixed, while the teeth of the lower jaw are brought forcibly against them with more or less of shock. And whilst these blows have to be received, resisted, and ultimately borne by the cranium, it is obviously desirable that they should be distributed over a sufficiently wide area, so as not to be felt unpleasantly.

The Maxillary Bone.—The ascending nasal process is very stout, and serves to connect the maxilla strongly with the frontal bone, which also in the region in question is powerfully developed; the thick malar process gives rigidity and resistance to lateral movements of the jaws, and carries off the strains to the lateral walls of the cranium; the maxilla is buttressed at the back by the pterygoid processes.

Thus, though the maxilla is hollowed out, so as to be lightened by the antrum and the nasal fossa, it forms a firm and resistant base against which to exercise force.

The alveolus of each individual tooth consists of a shell of comparatively compact bone of minute thickness, the *lamina dura*, which is imbedded in a mass of loose cancellous bone. This dense shell comes into relation with the dense cortical bone of the jaw mainly at its free margin, near to the neck of the tooth. Over very prominent roots, such as those of maxillary canines, a portion of alveolus is at times wanting, so that in a macerated skull the root is exposed to view.

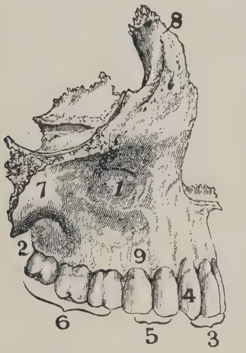

Fig. 21.—Superior maxillary bone of the right side. 1. Body. 2. Tuberosity. 3. Incisors. 4. Canines. 5. Premolars. 6. Molars. 7. Malar process. 8. Nasal process. 9. Alveolar process.

This difference between the bone constituting the immediate alveoli and that constituting the shell of the jaw-bones is very strongly marked in some mammals, notably in the manatee, in which there appears to be a continual migration of teeth forward taking place during the animal's life (see p. 497).

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CHAPTER II.

THE DENTAL TISSUES—ENAMEL.

Generally speaking, calcified teeth are composed of one or more structures which are in great measure peculiar to the teeth. Notwithstanding the existence of certain transitional forms, it is not possible to doubt the propriety of a general division of dental tissues into three, viz., Dentine, Enamel, and Cementum.

The first named of these constitutes the greater part of all teeth, and so far predominates in mass over the other constituents that, in very many cases, the tooth would nearly retain its form and character after the removal of the enamel and cementum.

This central body of dentine, enclosing the pulp, is very often covered by a cap of enamel, which forms the exposed surface of the tooth; this may be very partial, as in the eel or the newt, in which animals only this enamel-capped tip of the tooth projects far above the surface of the mucous membrane; or it may cover a much larger proportion of the tooth, as in man. Perhaps the most usual condition is that the enamel invests the whole crown of the tooth, terminating at about the level to which the gum reaches, as in the human and most other mammalian teeth of limited growth. In teeth of persistent growth the enamel extends down into the socket as far as the base of the tooth. In such cases it may embrace the whole circumference of the dentine, as in the molar teeth of many rodents, or it may be confined to one side only, as in their incisor teeth, where, by its great hardness, it serves constantly to preserve a sharp edge as the tooth is worn away. The enamel is believed to be quite absent from many teeth; thus the order Edentata, comprising sloths, armadillos, and ant-eaters, have it not; the narwal, certain cetaceans, some reptiles, and many fish also have none.

But although it might appear an exceedingly simple matter to determine whether a tooth is or is not coated with enamel, as a matter of fact in practice it is not always easy to be certain upon this point. When the enamel is tolerably thick there is no difficulty in making sections which show it satisfactorily, but when it is very thin it is apt to break off in grinding down the section. And even when it does not, it is in such cases usually quite transparent and structureless, and the outermost layer of the dentine being also clear and structureless, it is very hard to decide whether the appearance of a double boundary line is a mere optical effect due to the thickness of the section, or is indicative of a thin layer of a distinct tissue, which might be either enamel or cementum, for very thin layers of cementum look very much like enamel.

The author's investigations upon the development of the teeth of fish and reptiles have led him to suspect that rudimentary layers of enamel may exist upon many teeth on which their presence has not been recognised, for he has found that the formative enamel-organs universally occur, at least they exist upon all tooth-germs which have been adequately examined. Upon the teeth of snakes, which were stated by Professor Owen to be composed only of dentine and cement, he has endeavoured to show that a thin layer of enamel exists, and that there is no cementum. The frog has an enamel-organ as distinct as that of the snake, but it is not certain that there is enamel upon its teeth, although there is an appearance of a thin coat of distinct tissue. The armadillo has an enamel-organ, but observations have failed to discover any enamel or anything like it upon the adult teeth, and Professor Sir William Turner has made a similar observation upon the narwal.

At all events it may be said that in these and many other creatures no functional development of enamel probably takes place: whether it does or does not exist in an extremely thin and rudimentary layer has become a question of much less significance, since the author has shown the presence of an enamel-organ to be universal at an early stage.

Hence one may hesitate to endorse fully Sir Richard Owen's generalisation that dentine is the most and enamel the least constant of dental tissues; it is to be remembered that it may be so in completed teeth, but recent researches into dental development have very materially modified the conceptions formed as to the relations of the tissues to one another, and must lead one to examine carefully into such deductive statements before accepting them.

The remaining dental tissue is cementum, which clothes, in a layer of appreciable thickness, the roots of mammalian teeth, and reaches up as far as the enamel, the edge of which it may overlap to a slight extent, or entirely cover, or even not extend up to, so that when the cementum is present upon the crown it occupies a position external to that of the enamel. Cementum occurs universally upon the teeth of mammalia, but it is not always confined to the root of the tooth. In many teeth of persistent growth it originally invested the whole crown, and after it has been worn from the exposed grinding surface, continues to invest the sides of the tooth. (See the description of the complex teeth of the elephant, ox, horse, &c.)

It is probably entirely absent from the teeth of snakes, and indeed of very many reptiles; in the reptilian class, at all events, it would appear to be confined to those in which the teeth are lodged either in sockets or in a deep bony groove, as the author is unacquainted with any tooth anchylosed to the jaw in which it exists, unless one is inclined to include under the term cementum the tissue which has been designated "bone of attachment." (See "Implantation of Teeth.")

Chemical Constituents.—Upon the outer surface of the dentine the enamel forms a cap of a very much harder and denser material. In its most perfect form it is by far the hardest of all tissues met with in the animal body, and at the same time the poorest in organic matter. It has been usually stated that in the enamel of a human adult tooth there is from 3·5 to 5 per cent. of organic matter, but this is, as will presently appear, an error, there being probably only about 1 per cent. The calcium salts consist of a large quantity of calcium phosphate, some carbonate, and a trace of fluoride; in addition, there is a little magnesium phosphate.

Von Bibra (1) gives two analyses of enamel:

	ADULT MAN.	ADULT WOMAN.
Calcium Phosphate and Fluoride	89·82	81·63
Calcium Carbonate	4·37	8·88
Magnesium Phosphate	1·34	2·55
Other Salts	·88	·97
Cartilage	3·39	5·97
Fat	·20	a trace
Organic	3·59	5·97
Inorganic	96·41	94·03

Hoppe-Seyler (8), who believes that the salt mainly present in bone, dentine, and enamel is a compound salt, in which three molecules of calcium phosphate are combined with one of calcium carbonate, $Ca_{10}CO_3(PO_4)_6$ (just as in the mineral apatite two molecules of fluorine are combined with three of calcium phosphate), gives as his analysis:

$Ca_{10}Co_3(PO_4)_6$	95·35
$Mg.\ HPO_4$	1·05
Organic substance	3·60

In 1899 F. Bertz published an Inaugural Dissertation (Würtzburg) on the chemical composition of the teeth. An abstract of this paper is given in the "Jahresbericht über die Fortschritte der Thier-chemie," vol. xxx., 1900, p. 457. Bertz gives the following table for the composition of the teeth of man and of the calf:

	MENSCHENZÄHNE.		KALBERZÄHNE.
	Dentin.	Schmelz.	Schmelz
Organic substance	29·15	6·822	16·56
CaO	38·18	50·224	44·243
MgO	1·508	0·732	0·955
P_2O_5	30·244	40·693	37·019
SO_3	0·378	0·296	0·316
Fl	0·471	1·089	0·771
	99·931	99·856	99·864

The most recent analysis of dried enamel has been undertaken by Dr. Lovatt Evans (Proc. Int. Med. Congress, 1913, Section XVII.), who finds in 3·659 grm. of human enamel 39·56 c.c. of gas consisting of carbon dioxide 30·21 c.c. and nitrogen 9·35 c.c., thus giving a percentage of 0·55 carbon and 0·4 nitrogen, and in elephant enamel a percentage of 0·97 carbon and 0·57 nitrogen. His results therefore show that the organic matter in dried human enamel probably amounts to between 1 and 2 per cent., and in elephant enamel over 2 per cent.

[In this connection it may be pointed out that Mummery is of opinion that the 1 to 2 per cent. of organic matter found by Lovatt Evans would be quite sufficient in amount and accord with his views as to the histological evidences of the presence of organic matter in enamel.]

A large number of other analyses have been from time to time published, in which the proportion of organic matter ranges from 2 to 7 or 8 per cent.

The author undertook a series of experiments with the object of ascertaining what the nature of this organic matter was (18), but failed to discover, in any notable quantity, any substance giving proteid or proteoid reactions.

It is expressly stated in describing some of the published analyses that the organic matter was estimated simply by the loss on ignition, and this appears to have been the case in all, for in none of them is water set down as a constituent of dried enamel.

Hoppe-Seyler's statement that infantile enamel contains more organic matter, and otherwise differs from adult enamel, has been cited as an argument that enamel is not outside the pale of nutrition. But this argument is inapplicable, for his observations do not relate to the complete enamel of erupted teeth. He used the teeth of a newly-born infant, whose teeth were not erupted and whose enamel was far from being complete. It is difficult to see how it would be possible to obtain such enamel in adequate amount for certain analysis, and to be at the same time sure that it was quite free from adherent dentine and enamel-organ. Hence his analysis of infantile enamel is omitted in detail, as it appears so open to fallacy.

But the author's original analyses showed that in the case of elephant's enamel, which was selected because, on account of its thickness, it was comparatively easy to get tolerably free from adherent fragments of dentine or cementum, there was as much as 4 per cent. of water left after the enamel had been long dried at a temperature of 300° F. This water, which was apparently held in somewhat close chemical combination, was, under ignition, given off suddenly, and with such violence as to cause the fragments of enamel to crepitate and fly to pieces, and it was possible to collect it in a chloride of calcium tube and to weigh it, so as to prove that the total loss on ignition was very nearly accounted for by the water given off.

It would be out of place to repeat here in detail all the experiments, as they are to be found in the paper referred to (¹); it will suffice to say that probably there is no organic matter at all (in any noteworthy amount) in enamel, and that that which has heretofore been set down as organic matter, because it was lost on ignition, is simply water combined with the calcium salts.

When fragments of enamel are ignited in a hard glass tube, it is seen that the surfaces which had lain in contact with dentine or cementum become blackened, but that fractured surfaces in the midst of the enamel do not blacken at all but remain snowy white; it is thus shown that the very minute traces of organic matter found are mainly due to the practical impossibility of getting enamel quite free from adherent dentine or cementum, a conclusion which is confirmed by the microscopic examination of the trifling residue left when such enamel is dissolved in acids.

As a check experiment a solution of dissolved dentine matrix was prepared, and this was added to a solution of enamel salts so as to introduce $\frac{1}{4}$ per cent. of organic matter; this gave abundant proteid reactions. It has long been a familiar fact that enamel treated with acid disappears, whereas the organic matter in the prismatic layer of the shell of the mollusc *Pinna*, which bears a superficial resemblance to enamel, retains its structure and is actually more bulky than before decalcification, although it only amounts to 1·3 per cent. of the weight of the shell employed.

Enamel is then to be regarded as an inorganic substance composed of calcium salts which have been formed and deposited in particular patterns under the influence of organic tissues, which have themselves disappeared during its formation.

A very minute trace of organic matter is sometimes to be extracted by maceration of powdered enamel in caustic potash or baryta water, the subsequent addition of acetic acid producing a cloudiness; the quantity obtainable is far too small for identification, but the reaction above mentioned would indicate that it was either mucin or nucleo-albumin; it might have been derived from the fluids of the mouth, but in any case is in too small amount to be of much significance.

The rods of enamel, obtained by scraping or crushing, hardly undergo any alteration in form or appearance by ignition, except that they become a little more granular; but this slight amount of alteration seems to go to confirm what has already been said as to the absence of organic matter, for the expulsion of the combined water might easily cause a slight difference in the appearance of the crystalline salts.

The water is probably combined with the calcium phosphate; tribasic calcium phosphate when prepared by any wet method retains, in combination, one or more equivalents of water, which it will not part with below red heat, and the author's analyses show the presence of water in about (though not absolutely exactly) the proportion of one equivalent. This slight discrepancy, there being a little too much water, may be due to enamel being from its physical structure very difficult to dry absolutely; or perhaps some of the calcium phosphate retains two, and the rest only one equivalent of water.*

Distribution.—Enamel is of very common occurrence in the teeth of fish, reptiles and mammals, and is also to be found upon many dermal scales in fish; this is only to be expected, as the occurrence of an enamel-organ in early development is absolutely universal. But it varies in amount, forming sometimes a complete coating, sometimes a very partial investment, sometimes a mere spear point to give sharpness to the tooth, and sometimes it appears to be wholly absent.

In teeth of limited growth it terminates at the neck of the tooth, where it overlaps or is slightly overlapped by or fails to reach the cementum. Of these variations of termination it would appear that, as a rule, the two tissues actually meet one another. Choquet has found that in 27·5 per cent. of specimens he examined there was a breach of continuity, a minute surface of dentine being exposed. Where there is a complete coat of cementum over the crown this always lies outside the enamel, which is then between the cementum and the dentine.

The cap of enamel on a human tooth is of varying thickness, being thicker in the neighbourhood of the cusps than elsewhere.

Its outer surface is finely striated, the striæ being transverse to the long axis of the crown. They are called "*imbrication lines.*" In addition to this fine striation there may be a few deeper and more pronounced grooves, or pits, which are pathological and are marks of checks in development more or less complete. The enamel of some animals is almost structureless. Such is the nature of the little caps which, like spear points, surmount the teeth of some fishes, and which from their extreme brittleness are often lost in preparing sections, so that their very existence has long been overlooked. Some of these enamel tips, however, present an appearance somewhat similar to the enamel of *Sargus* (p. 67). But the absence of structure is after all a mere question of degree: in the commonest form of enamel, such as that of the human teeth, there is a finely prismatic structure, very apparent in imperfect teeth but far less so in well-formed ones, so that even when constituent rods cannot be distinguished this is merely an indication that calcification has progressed a little farther than in human teeth: if calcification only goes far enough, all structure, if not destroyed, might at all events be masked from sight.

Histology of Normal Enamel.—The structure of human enamel has been called fibrous; that is to say, it has a cleavage in a definite direction. and is capable of being broken up into columns or rods, which seem in transverse section to approximate more or less closely to pentagonal or hexagonal forms brought about by their mutual apposition. The rods run from the dentine towards the free surface; this is, however, subject to many minor modifications. The curved and decussating course of the human enamel rods renders it difficult to trace them throughout their length, but the structure of the enamel of many lower animals (especially the rodents) is more easily intelligible. Enamel such as that of the manatee, in which all the rods pursue a perfectly straight course, is of comparatively rare occurrence, but among the rodents the courses pursued by them are simple, and produce very regular patterns, which are constant for particular families.

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* [My friend Professor Gowland Hopkins, F.R.S., tells me that the literature on the chemistry of the teeth is fairly fully given in the "Handbuch d. Biochemie," by Hans Aron (1909), but I have not been able to obtain a copy of this work.—H. W. M. T.]

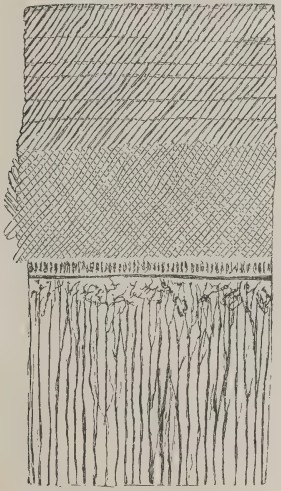


FIG. 22.—Transverse section of dentine and enamel of a beaver; in the inner half the rods of contiguous layers cross each other at right angles, in the outer they are parallel. Owing to the peculiarity of the direction in which they run in this animal, this figure has for clearness been rendered somewhat diagrammatic.

It is obvious that a transverse section, in order to show the decussation of superimposed layers clearly, must be parallel with the layers, *i.e.*, at an angle of 60° with the long axis of the tooth. But this obliquity will not be right for the outer portion in which the rods are yet more inclined upwards. Hence in the figure this has been corrected, and the simpler outer layer drawn as though the plane of the section were really parallel to the fibres in both layers.

The reader is requested to ignore the parallel lines in the upper portion of the figure, which are due to an unsuccessful attempt to represent appearances actually seen in a single section.

Thus in the *Sciuridæ* (squirrel family) a section of this tissue, whether longitudinal or transverse, appears divided into an outer and inner portion, in which the individual rods, although continuous from the dentine to the free surface, pursue different directions. As seen in longitudinal section, the enamel rods start from the dentine at right angles to its surface, and after passing through about two-thirds of the thickness of the enamel in this direction, abruptly bend upwards, forming an angle of 45° with their original course. In the inner two-thirds as seen in transverse section, they are found to be arranged in horizontal layers, each layer being a single rod in thickness; in successive layers they pass to the right and to the left, crossing those of the next layer at right angles, and thus making a pattern of squares in the inner two-thirds of the enamel. But in the outer third, where the rods bend abruptly upwards, those of superimposed layers no longer pass in opposite directions, but are all parallel; in fact no longer admit of distinction into alternate laminæ. Thus each layer of enamel rods passes in a very definite direction, and, seen with those of other layers, forms a very characteristic pattern; but the enamel rods are not in any part of their course curved.

In the beaver (*Castor fiber*) the course of the rods is not quite so simple. Examining a longitudinal section first, instead of the rods starting off at right angles to the surface of the dentine, they at first are inclined upwards towards the apex of the tooth at an angle of 60° with the dentinal surface; then, after passing through about half the thickness of the enamel, they turn up abruptly again, so that they here make an angle a little less than 30° with the dentine.

It follows from this that no one transverse section can show very plainly the direction of the rods in both parts of their course. The most instructive transverse section is one cut parallel with the layers near to the dentine; this will plainly show the successive layers passing to the right and to the left as in the squirrel, but the yet more inclined fibres of the outer half of the enamel will be cut across obliquely; for this reason the figure here given may be regarded as so far diagrammatic that the effect of this obliquity of cutting has been partly corrected, and the figure compounded from two sections, in each of which one set of rods was parallel with the plane of the section. It is still further complicated by the fact that the outer layers are not only inclined upwards but also sideways towards the middle line of the head; thus the middle line of the head would be to the right of the section as represented. As regards the decussation of the rods of alternate layers, it is similar to that of the *Sciuridæ*, but it differs in the laminæ being slightly flexuous instead of pursuing perfectly straight lines.

In the porcupine family (*Hystricidæ*) very much more complex patterns are met with, the enamel rods being individually flexuous, and their curves not confined to one plane; the individual rods pursue "a serpentine course forming three tolerably uniform curves," and cannot be followed far in any one section. Near to the surface, however, they all become parallel, the enamel thus conforming with that of other rodents in being divided into two portions (at least so far as the course pursued and the pattern traced by its rods in its inner and outer parts can be said to so divide it).

The *Leporidœ* (hares and rabbits) form an exception; their enamel has no such lamelliform arrangement, but is built up merely of slightly flexuous columns.

By tracing the courses of enamel rods from the simple pattern found in the manatee through that of the squirrel, beaver, and porcupine, it is seen how a very definite arrangement, at first simple, becomes modified into something a little more complex, till at last it reaches a degree of complexity that looks like mere disorder. No one unfamiliar with the enamel of other rodents, looking at the enamel of the porcupine, would be able to unravel the very indefinite-looking structural chaos before him; but had he studied forms in some degree transitional he could not doubt that the tortuous, curving course which he saw the rod to be pursuing was nevertheless perfectly definite and precise, and formed part of a regular pattern. It is very usual for the individual rods, like dentinal tubes, to pursue a spiral course.

In well-formed human enamel the rods are not very strongly marked, it being only in imperfect enamel that they are pronounced, and it is stated by Otto Walkhoff ([21]) that in different groups of rodents there are gradations between sharply defined rods and an almost homogeneous structure. Speaking generally, the rods are well defined in Primates, Carnivora and Cetacea, whilst in marsupials they are seen with difficulty prior to the application of acid.

In human enamel on the whole the rods are parallel, and run from the surface of the dentine continuously to that of the enamel. Their paths are not, however, either perfectly straight or perfectly parallel, for alternate layers appear to be inclined in opposite directions, while they are also wavy, forming several curves in their length. The curvature of the enamel rods is most marked upon the masticating surface; while on the sides the layers, alternating in the direction of their inclination as just described, are in planes transverse to the long axis of the crown, and correspond to the fine imbrication lines on the surface of the enamel, which appear to be caused by the outcrop of these layers. The curvatures take place in more than one plane; in other words, the course of the individual rod is more or less a spiral.

Although most rods run through the whole thickness of the enamel, yet inasmuch as the area of the outer is much larger than that of the inner surface of the enamel, and the individual rods do not undergo much alteration in size as they pass outwards, many supplemental rods are present in the outer portions which do not penetrate far inwards.

[This view is supported by Hopewell-Smith and by Howard Mummery. The latter has demonstrated the existence of supplemental prisms situated between the branchings of the main prisms in the enamel of the large third molar of the wart-hog (*Phacochœrus*) (Fig. 23), and concludes that the probabilities in favour of the existence of a similar condition in human enamel are great. On the other hand, Pickerill (15) contends that the existence of supplemental prisms is entirely unsupported by evidence, and, moreover, that their existence is negatived by comparative measurements of the enamel and prisms at the amelo-dentinal and free surfaces respectively. These measurements show that the prisms increase in size as they pass outwards, and that the ratio of their dimensions at the two extremities almost exactly corresponds with the ratio of the surface area of the enamel.]

The actual structure of enamel, which might have been thought to be a sufficiently simple matter of observation, is even yet not settled. It is an example of the difficulties which beset any observation of structures which have a high refractive index, being difficult to reduce to extreme thinness. Deceptive appearances may arise from the thickness of the section, from diffraction lines and other effects, from other than critical illumination, and from the smallest alteration of focus, so that with high powers there is always left a doubt as to the proper interpretation of that which appears to be seen.

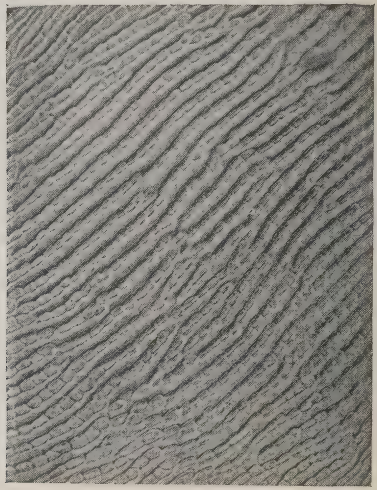


Fig. 23.—Enamel of *Phacochœrus* (wart-hog), showing branching of enamel prisms. (From a microphotograph by J. Howard Mummery.)

The rods of human enamel are about 5μ in diameter, though in places they may exceed this a little.

The individual rods are, under a low power, to all appearances structureless in perfectly formed human enamel, but a faint transverse striation, fainter, but otherwise not unlike that of voluntary muscle, is so general that it cannot be regarded as pathological, although it is most strongly developed in imperfect brownish enamel. The striation in question may be seen even in a single isolated rod, and is not necessarily continuous over adjacent columns, though it generally is so ; it is rendered more apparent by the slight action of diluted acids upon the rod. The striæ are from 3μ to 6μ apart. Very various interpretations of this appearance have been given. It has been attributed to "an intermittent calcification" of the enamel rod (Hertz), but is with more probability referred to varicosities in the individual rods (Kölliker, Waldeyer). It is very marked in the enamel of the common rat, which shares with that of other *Muridæ* the peculiarity of having the individual rods almost serrated, those of adjacent crossing layers being fitted to one another with great exactness. In human enamel the adjacent rods, if united without any intermediate cementing medium, and pursuing courses slightly different, must of necessity be of slightly irregular form, or else interspaces would be left, which is not found to be the case. Thus the "decussation of the rods" seemed a plausible explanation of this appearance of striation ; indeed, individual rods do present an appearance of slight varicosities, repeated at regular intervals. That the striation of enamel rods is due to this cause is confirmed by Febiger, an American expert in the resolution of diatoms, to whom enamel sections were submitted for his opinion by Dr. Xavier Sudduth. That the striation of voluntary muscle is due to such varicosities has been strongly urged

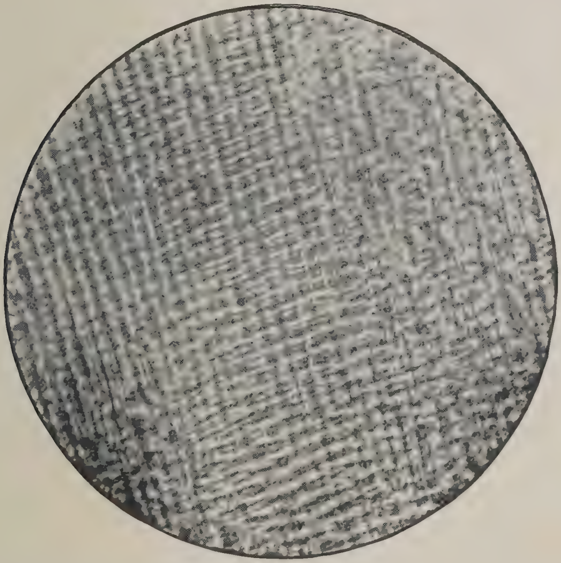


Fig. 24.—Striation of human enamel (from a photograph by Mr. Leon Williams). The specimen was ground fresh, mounted in balsam, and not treated with acid.

by Dr. Haycraft (7), and this is confirmed by Professor Ewald, of Strasburg (6), who finds that by pressing muscular fibre upon a film of moist collodion that substance reproduces the striation, and that by overstaining with silver nitrate, so that the fibres are rendered absolutely opaque, it may be shown by reflected light, the surface appearing to be made up of regularly recurring hills and valleys.

Von Ebner (5), however, holds that the cross striæ are due to the action of weak acid, and that the reason that they are seen in dry sections is that the Canada balsam in which they are usually mounted has a feeble reaction, and says that a similar etched pattern may be produced by acids on some crystals.

He does not, however, infer that the rods are therefore necessarily crystalline, but only that there are physical differences in their different parts; but this is controverted by Leon Williams and others, who have found the striæ without acids or balsam being used.

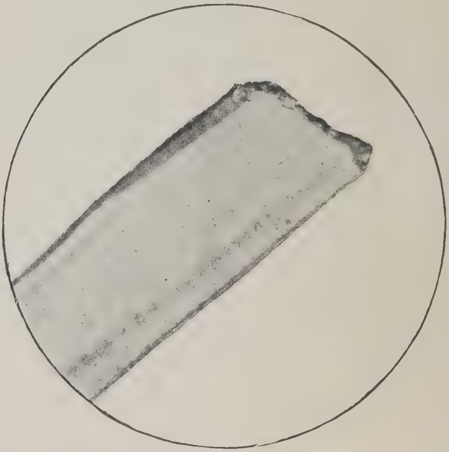


FIG. 25.—Isolated rod from the shell of *Pinna*, showing transverse striation (photographed by Mr. Mummery).

Transverse striation apparently due to varicosities is also to be seen in the rods of *Pinna*.

The comparison with the shell of *Pinna* must not be strained too far. Nevertheless, the resemblance of this prismatic structure to an enamel with rods on a bigger scale is sufficiently close to be in some measure instructive, although the tissue is composed of carbonate and not of phosphate of calcium, and though nothing is known of its development. A transverse section of pinna shell shows the pattern produced by the approximation of the sharply defined rods, but it is not possible to make out the existence of a cementing substance.

But if a section be rubbed down and then fastened to a glass slide and subsequently decalcified *in situ*, the rods wholly disappear, the pattern being, however, still maintained by the organic honeycomb in which they lay, and by which, presumably, their form was moulded. If a piece of human enamel be similarly treated, nothing is left upon the slide, so that it is certain that, whatever may have been the case during its formation, when it is finished the organic matrix is gone. And here again the resemblance fails in many respects, for it is probable that the organic mould is of a quite different nature ; indeed, as will presently be seen, the author holds that no thoroughly distinct interstitial substance exists in enamel.

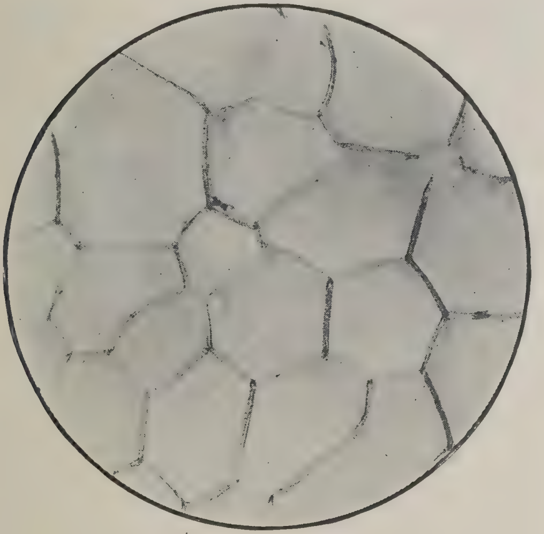


Fig. 26.—Decalcified matrix of pinna shell.

The researches of Leon Williams (22) have thrown much light upon the structure of enamel, and, illustrated as they are by very beautiful and untouched photomicrographs, must be accepted as, at all events, indisputable as respects that which can be seen, although exception might be taken to his statement that photography can show all that the human eye can see. In a sense this is true, though, as Professor Sir E. Sharpey-Schäfer has said, it is with one's finger on the fine adjustment that, after all, the intimate structure of any tissue must be unravelled. Still photographs have the unquestionable value that, unlike a drawing, they cannot be strained to express the preconceived ideas of the observer ; on the other hand, high-power photographs represent truly only one plane, and appearances due to other planes out of focus in the thickness of the section occur, to say nothing of diffraction errors which may mislead. He completely demonstrates that enamel is a solid tissue, that is to say, that the minute canals said by von Ebner to be present in it have no real existence, and that this observer is also mistaken in supposing that the striation is an artificial appearance induced by reagents.

Leon Williams believes that the completed enamel rod is a regular beaded calcified column, the beadings of which are the cause of the appearance of striation and that these beaded rods are embedded in a matrix which fills up all the interstices, is itself calcified, and does not differ much in refractive index from the rod itself. The varicosity of the rods and their consequent transverse striation is of variable distinctness; it is least seen, according to Leon Williams, nearest to the dentine.

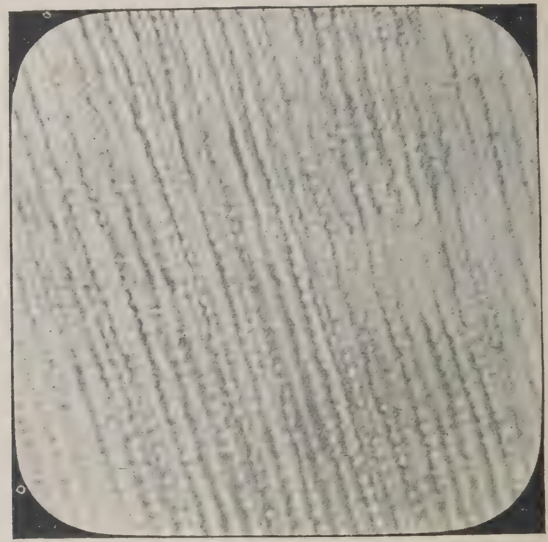


Fig. 27.—Human enamel washed with dilute hydrochloric acid (photographed and prepared by Mr. Leon Williams). The beaded appearance of the enamel rods is very clearly seen.

The difficulty of deciphering the intimate structure of a transparent calcified material is very considerable at best, and, to borrow an illustration from Leon Williams, in enamel it is much as though we had made a complex pattern with beaded glass rods, then embedded them in melted glass of a lower melting point, and then set to work to unravel the pattern of the original rods.

According to this observer, each rod is composed of more or less globular masses arranged at definite intervals and united in their lengths by smaller rods or bands. The rods thus built up touch, or almost touch, those around them, and the interstices, sometimes smaller, sometimes larger, are filled in with the matrix material. The varicosities in the rod lie in its length, and may be more or less fused together; those of one correspond with those of the next, and lie side by side, and do not interdigitate with them. On the subject of the ultimate constitution of enamel Leon Williams thus expresses himself: "The entire mass becomes so completely calcified that in normal mature enamel there is left no trace of organic matter. Only the original form remains duplicated in mineral substances like a fossil."

Such, then, are some of the views as to the nature of enamel, and they are confirmed by the action of orseille, a stain which will colour bone and dentine matrix without prior decalcification, but which fails to impart the smallest tinge to enamel.

But although both alike appear to consist practically of salts alone, there seems to be a little difference between the rods and the interprismatic substance, which may be chemical or may be merely physical, for under the action of acids the rods are at first rendered more distinct. Leon Williams believes that the acid acts first upon the interprismatic material, whilst other observers have thought the contrary; whichever be true, it is certain that the first effect is to render the rods more distinct in outline.

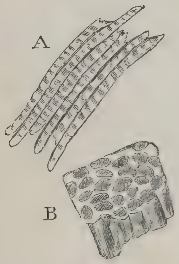


Fig. 28.—From human enamel, softened in chromic acid until it was friable. A. Longitudinal. B. Oblique section.

A curious phenomenon, rather inexplicable in the light of recent research, is sometimes, but not constantly, seen when enamel is subjected to the action of weak chromic acid (·25 per cent.): the striation is rendered very plain, and the axes of the rods are dark and stained green by the reduced chromium sesquioxide. But this appearance cannot always be produced at will (Fig. 28).

It has been already mentioned that the action of weak acids is to render the rods more distinct, and the nature of their union with one another and of the interstitial substance, if there be one, has led to much discussion.

Bödecker (3), basing conclusions upon the examination of thin sections stained with chloride of gold, held that enamel is built up of columns of calcified substance, between which minute spaces exist filled by a material which takes the stain deeply. He states that it gives off exceedingly fine thorns, which apparently pierce the rods at right angles to their length, so that it forms a close network very intimately mixed up with the calcified portion of the tissue.

It is not of uniform thickness, but is beaded, and Bödecker attributes to it a rôle of far greater importance than that of a mere cementing substance, for he regards it as being an active, protoplasmic network, which renders the enamel much more "alive" than it had hitherto been considered to be. He considers it to become continuous with the soft contents of the dentinal tubes through the medium of large masses of protoplasmic matter, which he believes he found at the margins of the enamel and dentine.

On this Klein (10) remarks that, "the enamel cells, like all epithelial cells, being separated from one another by a homogeneous interstitial substance, it is clear that the remains of this substance must occur also between the enamel rods; in the enamel of a developing tooth the interstitial substance is larger in amount than in the fully formed organ. It is improbable that nucleated protoplasmic masses are contained in the interstitial substance of the enamel of a fully formed tooth, as is maintained quite recently by Bödecker."

Von Ebner (5), who has investigated the histology of enamel, holds that there is an uncalcified cement substance between the rods, which appears to be traceable into continuity with Nasmyth's membrane, which latter, however, acids cause to become detached, so that this continuity may be merely apparent.

Bödecker's views have, however, never obtained much credence, and the result of Leon Williams's observations seems to dispose completely of them, as also of those of von Ebner, the appearances being explicable without the assumption of the presence of a noteworthy amount of organic matter. Many stains, and notably chloride of gold, will stain crevices even in mineral specimens, so that too much reliance must never be placed on the results of the reactions of stains alone. And the writer's own analyses, proving that there is no organic matter or only the most minute trace of organic matter in completed enamel, render it difficult to accept the existence of a complete network (cf. p. 40).

In a more recent address Leon Williams combats the explanation offered by Walkhoff, that the double contour seen in longitudinal sections is an optical effect, and reaffirms his belief in an interstitial substance between the rods, or "fibres" as he prefers to call them.

In transverse sections he has photographed the rods as being more round than hexagonal or pentagonal, so that there must be interspaces of necessity, and his skill as a microscopist is such that no one is less likely to be deceived in observation. Mummery also states that hexagonal rods are rarely seen in human enamel, but are much more constant in marsupials. Yet such are the tricks that high powers may play in producing deceptive appearances of things which do not exist that a shade of doubt must always remain. He holds, however, most strongly that whatever is between the rods is calcified, and does not contain organic matter in any quantity.

In fractured enamel, the line of fracture is said to run through the centre of the rods, and not, as might have been expected, through their interspaces.

There is also an appearance of striation upon a far larger scale, consisting of brownish lines, which are seldom, if ever, quite parallel with the outer surface of the enamel, but which nevertheless preserve some sort of relation with it and the surface of the dentine.

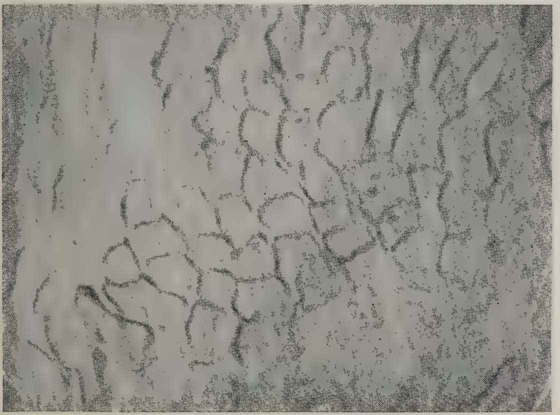


FIG. 29.—Thin ground section of human enamel, showing rods cut in transverse section. Unstained. (Microphotograph by Bowdler Henry.)

In vertical section these lines have the appearance of brown arcuate stripes, the more complete ones commencing at the amelo-dentinal junction on one side, arching over the peak of the dentinal cusp, and terminating at a similar point on the opposite side; the less complete pass obliquely outwards and end at the enamel surface. In horizontal section they are seen as concentric rings darker and more pronounced towards the periphery.

These lines are known as the " brown striæ of Retzius," and, as they coincide with what was at one time the outer surface of the enamel cusp, are in some sense marks of stratification in its original deposition.

Von Ebner suggests that they are due to the entrance of air into spaces between rows of enamel rods, but this is strongly controverted by Leon Williams and others, who not only deny the existence of spaces into which air could enter, but have shown [the lines to be present in preparations of teeth which have never been allowed to dry, as in the Weil method. Underwood asserts that excessive granularity is the cause, and, as the granularity in each prism corresponds with that of its neighbour, the effect of a line is produced. His view of the relatively deficient structure of the prisms in the striæ seems to be confirmed by the fact that in hypoplasia, where the enamel is admittedly ill formed, the striæ appear more pronounced and converge below the "pits" into a densely brown structureless mass. Leon Williams and Hopewell-Smith support the view that pigmentation is responsible; but Pickerill refutes this by stating that when enamel is pigmented, as may happen occasionally in pathological conditions, the pigment is evident, however it be viewed, and is more intense by reflected light than by transmitted light; whereas the "brown" striæ, when examined by reflected light, appear intensely white. He regards the phenomenon as being due to increased optical density of the prisms, but whether this is brought about by greater consolidation or excessive granularity is not stated. Pickerill's reference to the white opacity in incipient dental caries of the enamel, where the rods are partially disintegrated, would seem in some measure to support Underwood's view.

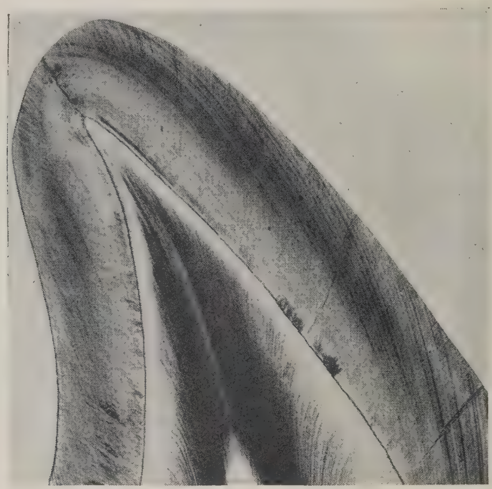


Fig. 30.—Vertical section of the tip of an incisor tooth, showing well-defined "brown" striæ of Retzius. (Microphotograph by Bowdler Henry.)

Whatever the causation—be it due to an alternation of pigmented with non-pigmented layers of enamel, or to the alternation of segments of prisms of varying degrees of granularity—the appearances suggest the intermittent nature of the development of enamel, and the terms proposed by Pickerill of "lines of growth" or "incremental lines" may be more definitive.

As has been stated (on p. 42), there are just visible to the naked eye on the dried surface of the enamel of human permanent teeth fine corrugations, called "imbrication lines." These can be demonstrated by rubbing firmly the surface of the tooth with fine graphite and photographing it by reflected light, as has been done by Pickerill (15). The depressions retain the graphite, whereas the elevations remain white. All teeth treated in this manner show exceedingly fine black bands (the depressions) encircling the crown, and are most marked interstitially just below the point of contact. Further evidence of these corrugations is to be seen on the deep surface of the pellicle of Nasmyth's membrane, which, when fixed and stained with a 5 per cent. solution of nitrate of silver and floated by means of nitric acid, exhibits dark bands corresponding to the furrows and produced by reason of the pellicle in these places being a little thicker than over the elevations. This is confirmed by Howard Mummery, whose preparations show that the deep surface of the membrane is not only impressed by the ridges, but that superimposed upon these are the minute impressions in lineal series of the ends of the enamel rods. The relationship of these imbrications to the brown striæ of Retzius is shown in vertical sections of enamel examined by reflected light. In such sections the surface corrugations can be clearly seen; and, as shown by Pickerill, each elevation appears to be the outcrop of a stria of Retzius or stratum of enamel prisms.]

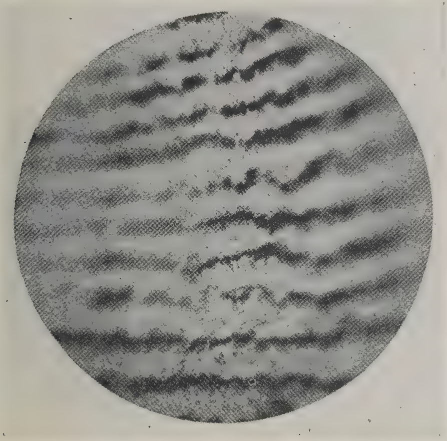


FIG. 31.—Surface of enamel treated by the graphite method, showing the imbrications, from a point half-way up the crown of a tooth. (After Pickerill, "Dental Cosmos," Vol. 55, 1913.)

It has been suggested by Zsigmondy (23) that they are due to actual imbrications of the ends of the enamel columns, being thus produced by the grinding down of a longitudinal section.

There is another class of markings seen upon the surface of a section of enamel, known as "Schreger's lines." These are dependent upon the different directions of contiguous groups of rods, and can be seen by reflected light, when they appear as light feathery bands, and by transmitted light, when they assume a dark aspect.

[Starting from the amelo-dentinal junction, Schreger's lines pass outwards towards the enamel surface, and curve in their upward course slightly towards the incisive edge. They are viewed best in vertical sections under low magnification, and they may even be seen by the naked eye with reflected light.

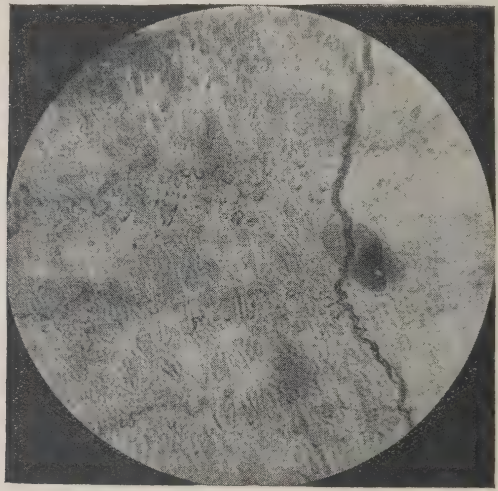


Fig. 32.—Floated preparation of Nasmyth's membrane, showing impressions of enamel prisms in parallel lines. × 250. (From a microphotograph by Mummery.)

Hopewell-Smith states that all sections do not exhibit them, and von Ebner says that they are quite invisible by transmitted light. In thin sections this would appear to be the case, but Pickerill asserts that he has not seen a section which did not show them distinctly by reflected light.

There is equal diversity of opinion also as to their causation. Pigmentation and polarisation of light have been suggested, but it is probable that Pickerill's conclusion is more correct, namely, that the effects are produced by the different optical densities of contiguous groups of prisms. Howard Mummery is also of the opinion that they are due to optical phenomena and have little histological importance.

The amelo-dentinal junction appears as a dark irregular line due to minute convexities of the enamel.] A few cavities, or at least what look like cavities, of irregular form, often exist in the coronal enamel close to the surface of the dentine, jutting out, as it were, from the amelo-dentinal junction, and the dentinal tubes sometimes communicate with them. Hopewell-Smith calls them "enamel spindles." Perhaps these are to be regarded as abnormal, but they are very common, [and, as observed by Mummery, they are seen in well-formed teeth sound in other respects, and are conspicuous in the densely calcified enamel of the teeth of prehistoric man. Seen in vertical-radial sections, they are disposed with some regularity about the margins of the underlying dentine cusps. An examination of sections of enamel cut tangentially to the amelo-dentinal junction exhibits the "spindles" cut transversely, but, instead of appearing as dots, as they would if they were of tubular form, they appear as "sinuous lines fringed at the margins." Pickerill, who described this appearance, regards them as interprismatic spaces coupled with defective development of the cement and of the outer portions of the prisms. Further, he states that the dentinal tubules do not enter the spindles, and ascribes the appearance of continuity to artifact. The significance and the causation of enamel spindles is obscure.] Römer says that they have organic contents in the fresh state, and suggests that they contain nerve endings. Bödecker, of course, regards them as filled up by proto-

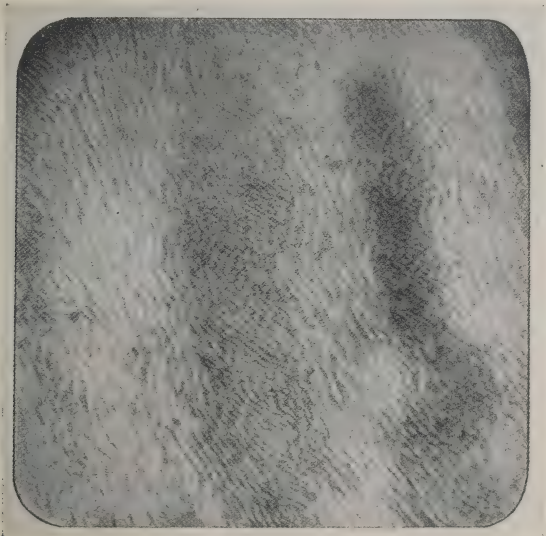


FIG. 33.—Vertical section of human enamel, showing the lines of Schreger. Section ground thin. Unstained. × 250. (After Hopewell-Smith, "Dental Histology," 1903.)

plasm. Walkhoff considers that prior to enamel deposition the surface of the dentine is absorbed, and that they are dentine tubes left unabsorbed—an unlikely hypothesis. [Howard Mummery describes their contents as dark amorphous granular matter, but some spaces are "quite clear and transparent and, when stained from the dentine by the fuchsin method, show a clear uniform coloration." He seems to agree with Pickerill that the spaces are imperfections in the calcification of the interprismatic substance, but maintains that there is in many cases a direct communication between them and the dentinal tubes. According to Mummery, the dentinal tubules may either terminate in those spaces or, passing through them, penetrate more deeply into the enamel. The spaces are not mere dilatations of the tubes; and, as Mummery writes, "it is significant that in those marsupials in which the tube system is much reduced, bodies exactly like the spindles in human enamel are found at the amelo-dentinal junction."]

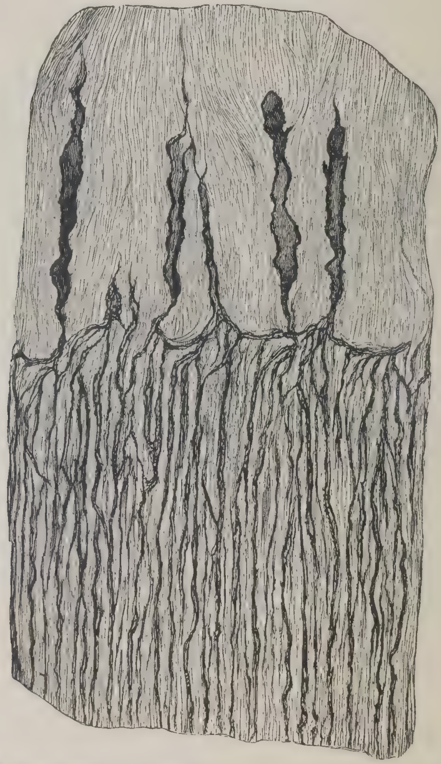


FIG. 34.—"Enamel spindles," which communicate with the dentinal tubes.

Irregular fissures and spaces also occur upon the outer surface of the enamel, which also have no special significance save, perhaps, as predisposing causes of dental caries.

Tubular Enamel.—In man, however, dentinal tubes may occasionally be seen to enter the enamel, passing across the amelodentinal junction and pursuing their course without being lost in irregular cavities. As was first pointed out by Sir John Tomes, the passage of tubes continuous with the dentinal tubes into and through a great part of the thickness of the enamel takes place in marsupials with such constancy as to be almost a class characteristic.

The only exception to the rule amongst recent marsupials occurs in the teeth of the wombat, in which no dentinal tubes enter the enamel; those extinct marsupials which have been examined present, as might have been expected, a structure in this respect similar to that of their nearest allies amongst the recent genera.

The enamel of the wombat is peculiar also in another respect, in the fact that it is covered by a strong and remarkably uniform layer of cementum.

The penetration of the enamel by dentinal tubes is not, however, a peculiarity quite confined to the marsupials, for it is to be found in some rodents (*e.g.*, the jerboa), and in some insectivores (*e.g.*, the *Soricidæ*), and in many fish.

[A similar condition has recently been found by Thornton Carter (4) in certain genera of extinct Sparassodonts, *e.g.*, *Cladosictis*, *Pharsophorus*, and in *Borhyæna* (now generally regarded as a polyprotodont marsupial), as well as in the Creodont *Hyænodon*.]

Waldeyer and Hertz doubted the passage of the tubes of the dentine into the enamel; but, as Kölliker observes, it is difficult to see how they can doubt it, even after mere observation of a single specimen; moreover, it is also capable of experimental demonstration, for if an acid capable of removing the enamel be applied to one of these sections of marsupial teeth so as to dissolve away the enamel, the freed tubes are left hanging out from the edge of the dentine, thus putting the matter beyond all possibility of doubt. The penetration of the enamel by tubes continuous with the dentinal tubes seems rather common in fish; these tubes in the enamel grow smaller as they leave the dentine and do not reach the exterior of the enamel; examples may be found in *Serrasalmo*, in the barbel and in many extinct fish.

The author is of the opinion that the tubes, probably, run in the rods and not between them, though it has been stated by von Ebner that the tubes in marsupial enamel do not lie in the rods themselves but in their interspaces, and he gives a figure of a transverse section in which all but one of the tubes appear to do so. [Von Ebner's view is strongly supported by Mummery (11), who figures sections showing tubes of distinctly wider diameter than the prisms. He thinks that the tubes wind spirally round the prisms, being themselves placed in the interprismatic substance.]

Leon Williams has photographed some transverse sections of marsupial enamel, in which three-fourths of the tubes appear clearly to be in the substance of the rods. The remaining fourth appear as though they were between them. But it is *a priori* highly improbable that they occupy both positions, and a position within the rod is much more readily reconcilable with the appearances seen in the development of marsupial enamel (see p. 168).

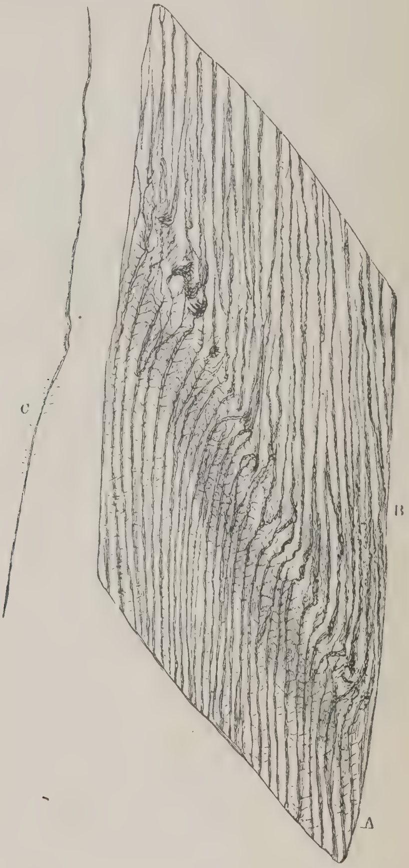


FIG. 35.—Enamel and dentine of a kangaroo (*Macropus major*).

The dentinal tubes in the dentine (A) are furnished with numerous short branches at the line of juncture with the enamel; they are dilated and a little bent out of their course, while beyond the dilatation they pass on through about two-thirds of the thickness of the enamel (B) in a straight course and without branches. Only a part of the whole thickness of the enamel is shown in the figure. C = an isolated tubule.

[However, the condition described by Leon Williams has been confirmed by Thornton Carter in the enamel of *Macropus*. To quote this investigator, he states that "the course of the enamel tubes and their occupying fibrils is not associated with or dependent upon the direction of the prisms: they may proceed parallel with the prisms, lying in the interprismatic area; or they may lie within the substance of the prisms; or they may proceed at right angles to or tangentially across groups of prisms."]

Although it has been usual to speak of marsupial enamel as penetrated by dentinal tubes, this is a somewhat improper use of terms. The enamel has a tube system, and its tubes are continuous with those of the dentine, but the tubes in the enamel are wholly and entirely an enamel formation, derived from the epiblast cells (see p. 171), which at the beginning of enamel development join up with the ends of the dentinal fibrils in the first-formed layer of dentine, or perhaps even earlier with the odontoblasts, before the formation of any dentine.

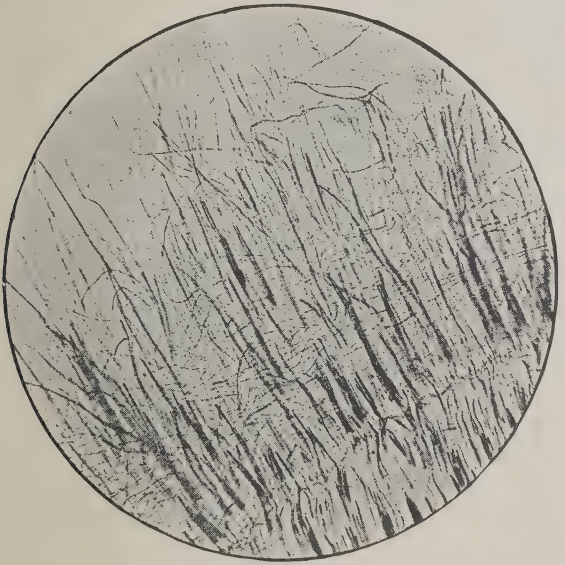


Fig. 36.—Enamel of *Lepidotus*, a ganoid fish existing from the Jurassic to the Tertiary periods; a small portion of dentine is seen at the bottom of the figure.

The penetration of enamel by tubes is met with in many fish, and some instructive examples may be met with in the sharks. In some fossil sharks and ganoid fish, *e.g.*, *Lepidotus*, there is a rich crop of tubes in the enamel which are continuous with those of the dentine, becoming curiously curved as they course through the inner half of the enamel, and lost before they reach its surface.

Doubt has been expressed by Dr. Paul whether the author was correct in describing the outer layer of the tooth of *Lamna* as fine tubed dentine, it being, in his opinion, more like enamel. Paul's criticism led to an examination of the teeth of *Selachia* which had unexpected results (^{14}).

It had not escaped the notice of older observers that the outer layer of the teeth of some ganoid and elasmobranch fishes differed from the more familiar dental tissues, and special names were applied to it, such as ganoin, vitrodentine, and placoid enamel. When it is thin, as in many rays, it looks like an ordinary enamel, but when it is thick it diverges both from the ordinary types of enamel and of dentine.

It resembles enamel in that it almost completely disappears under the action of an acid, no coherent matrix being left; it is highly refractive, is very hard, and will not stain, remaining white even when under the influences of fossilisation, the dentine matrix is stained dark brown by iron. It is not known whether any analyses of it are available, but it is noticeable, if it is watched while dissolving in an acid, that while copious bubbles are given off from the dentine, very few come off from the enamel, thereby indicating that the latter is poorer in carbonates.

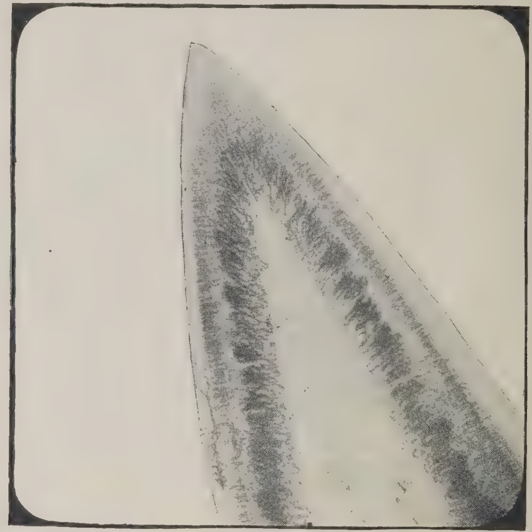


Fig. 37.—Tooth of *Lamna*. The outer layer, dark at its inner and transparent at its outer portion, is enamel; the centre core is dentine.

On the other hand, it is penetrated for some distance (in certain forms) by thin tracts of dentine matrix as well as by tubes: a lamination parallel with the surface can often be seen, a banded structure is visible in transverse section, and it often contains interglobular or lacunar spaces unlike any other known enamel. It thus participates in the characters both of dentine and enamel, though inclining more towards the latter, and its true position cannot be determined without reference to its development, which it would be premature to describe here. It may, however, be mentioned that whilst it is formed in a mesoblastic tissue, viz., the exterior of the dentine papilla, the cells of the enamel-organ appear to take an active part in its calcification, so that in its development also it is intermediate between the two tissues.

In *Galeus* (one of the *Lamnidæ*), the surface of the dentine is somewhat festooned towards the enamel; the dentine is of the osteodentine type (p. 103), and therefore not very richly tubular, but some tubes do enter the enamel. Not only do tubes enter the enamel, but by staining after slight washing with acid it may be shown that tracts of dentine matrix enter with them; this is common to all, but the depth to which these tracts penetrate, and their size, vary in different genera and families.

This at first sight would seem to lend probability to Dr. Paul's suggestion that the penetration of enamel by tubes continuous with the dentinal tubes in marsupials and others could be explained by the dentine matrix growing out into the enamel, and so carrying tubes in between the enamel rods. But, as has been shown elsewhere (19), this explanation is not true as regards marsupials, seeing that the tubes in enamel appear developmentally to belong wholly to the enamel (cf. p. 171).

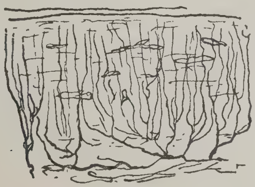


FIG. 38.—Enamel of *Galeus* (one of the *Lamnidæ*), showing penetration by tubes running in from the dentine.

Besides the tubes brought in from the dentine, the enamel of *Lamna* has a rich tube system of its own, these tubes being much coarser than the dentinal tubes, and about one-third of the way through the enamel they communicate with irregular lacunal spaces, a condition which has not been noticed in other enamel. These are both numerous and large, giving a confused appearance to this region; beyond it the tubes are continued on to the outer surface, near which there is a more or less differentiated layer. In *Galeus* this outer layer is much more distinct, and has every appearance of parallel tubes running in from the surface like those of *Sargus* (Fig. 45).

The varieties in the disposition of the tubes and of the lacunal spaces are almost infinite, and it is only possible here to instance a few; Jaeckel states that characters in the dentine, and especially in the enamel, are constant for genera or groups of genera.

A fossil shark from the London clay, not identified, is yet more interesting. In this specimen (Fig. 39), the enamel is quite white, but the dentine has taken a strong brown stain, and shows clearly that the festooning of the dentine surface is carried further than in *Lamna*, so that tracts of dentine, their tubes going with them, enter the enamel for a greater distance, somewhat less than one-third of thickness of this tissue, which is three millimetres thick.

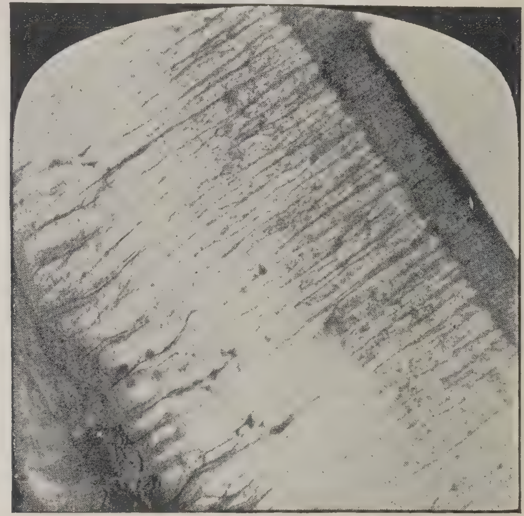


Fig. 39.—Enamel of a fossil shark, not identified, from the London clay. At the left-hand bottom corner is a small amount of dentine; at the right upper side of the enamel is seen the distinct outer layer in which there is an appearance of tubes entering from the surface.

[Röse (^{16}) argues against these tissues being regarded as enamel, and claims that an exceedingly thin layer of real enamel does exist over them as a glaze. My paper had not then been published, so that Röse had not before him the considerations which it contains, and the two papers were so nearly contemporaneous that I had not seen his when mine was first written, though it was published in time for me to refer to and consider it in my paper before its actual publication in the "Philos. Trans." (^{20}). As I can only claim the tissue as an enamel on the balance of considerations, and have presented facts which tell both ways, it is possible that I may not have made a convert of Röse. But, on his hypothesis, calcification ought to commence on the exterior and to advance inwards, the calcification of the core of osteo- or trabeculo-dentine only commencing when calcification has reached in to it. But that is not the case (cf. p. 179): the first calcification is the border line beneath this enamel layer, in fact, where enamel calcification ought to commence if this line be the outside of the real dentine, as I hold it to be. And I do not attach much importance to double refraction as a test, though when it is pronounced it is useful. In common with Röse himself, I have often seen it in undoubted dentine, so that it is an adjunct, but not an infallible test.

Of the disputed structure I wrote (*loc. cit.*): "It is seen to shine out brightly under dark ground illumination, its refractive index being high; and it is doubly refractive, though this does not stand for much, as the osteodentine in *Lamna* is also doubly refractive, and with polarised light shows a well-marked black cross intersecting the concentric laminæ round each Haversian system.—C. S. T.]

Whilst the tubes appear to run through the whole thickness of the enamel, they are larger near to the dentine and again near to the surface.

The differentiation of an outer layer, already noted as traceable in *Lamna* and *Galeus*, is much more marked in this London clay fossil; the figure, however, exaggerates it, as it is from a photograph and the layer was yellower than the rest of the enamel. Fine lacunar spaces exist along the inner margin of this belt, which shows a fine striation perpendicular to the surface. The thickness and distinctness of this outer layer vary in different Plagiostomes, it being quite absent in some of them.

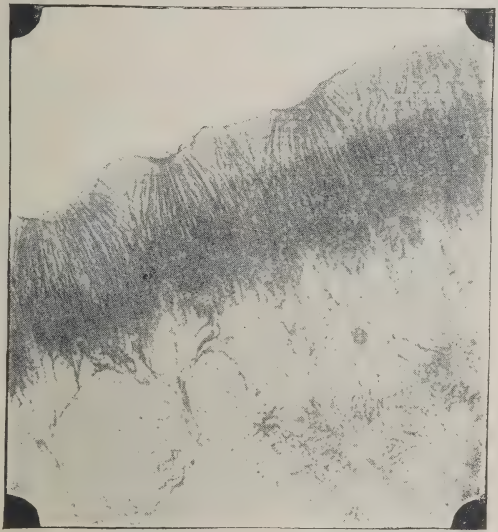


Fig. 40.—Enamel of *Heterodontus* (*Cestracion*); the lower part of the figure consists of vascular dentine.

Occasionally the striation of this outer layer is of such character that it has the appearance of tubes entering from the free surface.

The outer surface of the tooth of the archaic existing shark *Heterodontus* is very peculiar. The pattern looks like fine tubes running in from the surface, upon which they open with large mouths, and they are gathered into bundles, so as to make, as they radiate inwards, a well-defined pattern.

Analogy, and its development so far as it has been studied in somewhat imperfectly preserved material, lead to the inference that this corresponds to the enamel of other *Selachia*, and, possibly, only to the specialised outer layer just described.

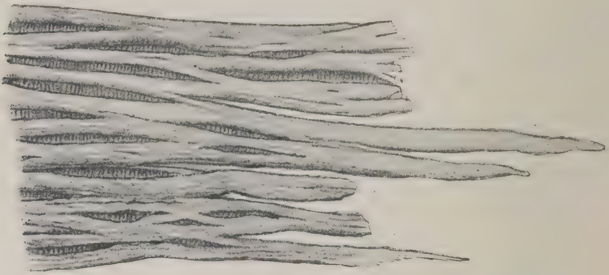


Fig. 41.—Transverse ground section of the enamel of *Galeus.*

Longitudinal sections of all these enamels show with varying distinctness a lamination parallel with the surface. Transverse sections show, in such as have been examined, a peculiar structure of bands which leave between them oat-shaped interstices; in these interstices are found to be the prolongations of dentine matrix

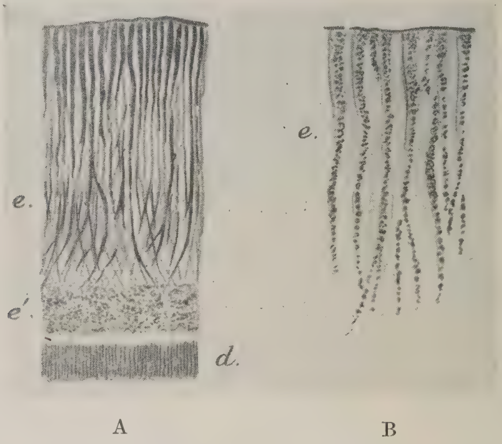


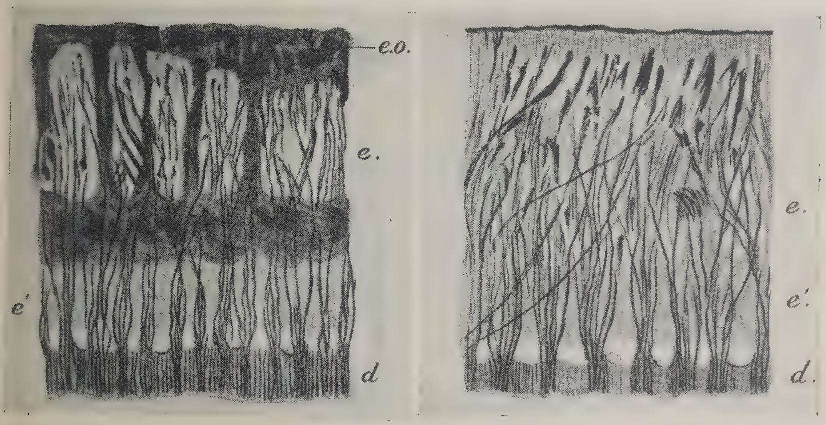
Fig. 42A.—Ground section of a fuchsin-stained, fully-erupted tooth of *Sargus ovis*, preserved in formalin. The stained tubes are seen communicating with the exterior; the stain penetrates the finest divisions, but does not enter the area of enamel at e'. × 50.

Fig. 42B.—From a similar preparation, showing granules in the tubes. From a photograph. × 200. (After Mummery, Phil. Trans. Royal Soc. Lond., vol. ccviii. B., 1917.)

already described. This structure is not found in any enamels or dentines hitherto described.

In *Sargus*, or the sheep's-head fish, and in various other fish, the enamel is penetrated by a system of formations which are not continued out of or derived from the dentine, but belong to the enamel itself.

These markings, as seen in the figure (Fig. 42), run at right angles to the external surface of the enamel, proceed inwards without branching for some little distance, and then, at about the same point, bend abruptly at an angle, and give off numerous branches. The meshwork produced by the crossing of the tubes at all sorts of angles in the inner part of the enamel is so complicated as to render it impracticable to reproduce it in a drawing. That portion of enamel next to the dentine is without any appearance of canals. Von Boas (²), describing similarly constructed enamel of scaroid fishes, says that the canals do not open upon the outer surface of the enamel. Though they have every appearance of being tubes, it is difficult to make coloured fluids enter them.



A B

Fig. 43A.—Ground section of unerupted molar tooth of *Sargus noct*, stained in bulk with alcoholic fuchsin by the capillary attraction method, before grinding. The dried remains of the enamel organ are seen at *e.o.*, very deeply stained; the stain passes into the enamel in broad vertical bands, which communicate with the broader horizontal coloured band, but does not penetrate into the layer of enamel at *e′*. The tubes from the dentine are strongly stained. From a photograph. × 50.

Fig. 43B.—From a similarly treated section of the completed enamel of *Sargus noct*. The majority of the stained tubes are cut off from communication with the exterior of the enamel in *Sargus noct*, where a tubular system from the dentine is fully developed. From a photograph. × 50. (Mummery, Phil. Trans. Roy. Soc. Lond., vol. ccviii. B., 1917.)

If a thin section be treated with dilute hydrochloric acid and watched during its action, short rods appear projecting from the surface, but they soon dissolve away.

[The structure of the enamel in the genus *Sargus* has recently been investigated in detail by Mummery (12). He has succeeded in causing alcoholic stains to enter the enamel tubules from the superficial striæ and pits, and finds that there are variations in structure in different species. Moreover, he concludes that the tubes contain a minutely granular material, and in the wider tubes he noticed the presence of additional deeply staining rounded bodies resembling the nuclei of red blood corpuscles.

In *Sargus ovis* the conditions are as just described, while in *Sargus noct* the enamel pattern is further complicated by a free and regular penetration from the dentine also, which may branch and terminate in spindle-shaped spaces below the enamel surface. The two systems of tubes interlace, and together with the spiral enamel prisms form a very complicated pattern of enamel. In the incisor teeth of *Sargus vulgaris* there is an intermediate condition. There is a penetration of both sets of tubes, as in *Sargus noct*, but those from the dentine enter in bundles, spread out in a radiating manner, and pass but a very short distance into the enamel, and terminate in a line of dense calcification.

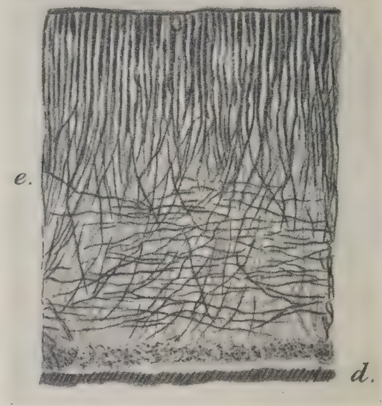


Fig. 44.—Stained ground section of upper pharyngeal tooth of *Scarus*. The stain has penetrated the vertically arranged tubes, but did not reach the horizontal ones. From a photograph. × 50. (Mummery, Phil. Trans. Royal Soc. Lond., vol. ccviii. B, 1917.)

Similar conditions were found to occur in *Chrysophrys*, *Pagellus*, and in the *Labridæ*. The most complete and complicated system of tubes from without is to be seen in *Scarus* (Fig. 44).]

All these forms of tubular enamel, especially those in which the tubes open on and enter from the surface, were very unintelligible, as it was hard alike to see what advantage they could confer upon their possessors, or how they were developed. But if the author's conclusions as to the development of enamel (cf. description of development of marsupial enamel) be accepted the difficulty of interpretation disappears. If all enamel in its development passes through a tubular stage, then these are merely arrests of complete development and perpetuations of a stage which is transitory in placental mammals.

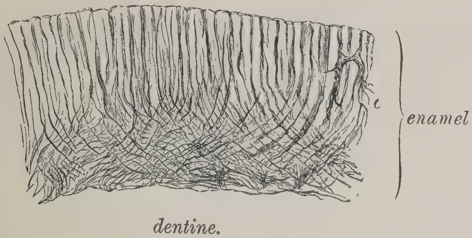


Fig. 45.—Enamel of the sheep's-head fish (*Sargus ovis*).

The enamel is penetrated by a system of formations, probably tubes, which enter from its free exposed surface, pass in for a certain distance in straight lines, and then, abruptly bending at an angle, cross one another, and produce a complicated pattern in the inner third of the enamel.

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(1) von Bibra. "Chemische Untersuchungen über die Knocken und Zähne des Menschen und der Wirbelthiezen, &c.," 1884. Schweinfurt.

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CHAPTER III.

ORTHO-DENTINE AND ITS VARIETIES.

The dentine constitutes the greater part of every tooth, which thus even after the removal of the other tissues, preserves somewhat of its characteristic shape. Several varieties exist in which those peculiarities of structure which differentiate it from bone are less marked, so that a point is sometimes reached at which it is hard to say whether a particular structure should more rightly be described as dentine or as bone. It will be most convenient to commence with a description of that variety of dentine which differs most markedly from bone, or, in other words, which has the most typical " dentinal " structure ; and for that purpose the tissue met with in the teeth of man and the majority of mammals (though it is by no means confined to that class), and known under the name of " hard " or " unvascular " dentine, may be selected. This may also be called " ortho-dentine."

Dentine is a hard, highly elastic substance, in colour white with a slight tinge of yellow ; it is to some extent translucent, its transparency being often made more striking by contrast with the opacity which marks the first advent of dental caries. When broken, a silky lustre is seen upon the fractured surfaces, which, being in the main due to the presence of air in its tubes, is more apparent in dry than in fresh dentine ; its fracture is sometimes described as finely fibrous.

The mass of dentine consists of an organic matrix richly impregnated with calcareous salts ; this matrix is everywhere permeated by parallel tubes, which radiate, with some minor exceptions, from the pulp cavity towards the surface of the tooth.

Chemical Composition.—The organic matrix of dentine, after the removal of the calcium salts by an acid, is a yellow material of cartilaginous consistence, which when dried is not unlike horn ; it is insoluble, and does not swell up in water, but dissolves when submitted to prolonged boiling, and is in fact converted into gelatine. It is similar to the substance obtained in like manner from bone, known as collagen, a substance with a highly complex chemical composition.

Collagen.—The white fibres of connective tissue, and the greater part of the organic matrix of bone, dentine and cementum, consist of this substance. Chemically it is nearly related to gelatine, of which it is the anhydride. By boiling in water for some little time it takes up an equivalent of water and becomes converted into gelatine; conversely, gelatine, by being heated to 130° C., may be dehydrated and converted into collagen, thus,

$$\underset{\text{(Gelatine)}}{C_{102}H_{151}N_{31}O_{29}} - H_2O = \underset{\text{(Collagen)}}{C_{102}H_{149}N_{31}O_{28}}.$$

Elastin is another albuminoid substance which is abundant in ordinary elastic tissue. It is very insoluble, but may be dissolved by concentrated sulphuric acid, or concentrated nitric acid, or hot caustic potash, which, however, all decompose it. The linings of Haversian canals, of the lacunæ and canaliculi, and the sheaths of Neumann, to be presently described, are probably composed of this substance. It contains no sulphur, and thereby differs from keratine, which in some respects it resembles. Though insoluble in any fluid which does not decompose it, it is slowly digested by pepsin or by trypsin.

When the decalcified matrix of dentine is boiled so as to form gelatine a small insoluble residue is left, and the same result may be attained by treating dentine with an acid sufficiently strong to bring the collagen into solution. A like effect is obtained with bone.

This residue, which consists of a material singularly resistant to the action of acids and alkalies, appears to consist of elastin. In ivory, which is a highly elastic form of dentine, the elastin amounts to about 2·7 per cent. of the dried decalcified matrix, and it is, without doubt, as can be seen by a microscopic examination of the residue above alluded to, derived from the immediate walls of the dentinal canals or sheaths of Neumann, of which this residue wholly consists.

As has been already pointed out in the case of enamel, an important error pervades the current text-book analyses of dentine. The usual method of estimating the total salts is by ignition, that is to say, after fully drying the tissue at 212° F., by burning away the organic matter, weighing the residual ash which contains all the salts, and computing the loss as organic matter. In this way from 69 to 72 per cent. of salts is generally found, and dentine is usually said to contain from 31 to 28 per cent. of organic matrix, the amount of the loss.

But if, instead of doing this, the calcium salts are dissolved out and then the collagen dried and weighed, it will be found that it falls far short of this, only amounting to about 19 per cent. of the dried dentine. The cause of this discrepancy, which has been long overlooked, is that dentine fully dried at 212° F. still contains something like 8 per cent. of water, which was held in chemical combination with the calcium salts, and can only be driven out at red heat; in fact, the calcium phosphate, like any calcium phosphate prepared by wet methods, holds in combination one or more equivalents of water.

Thus fresh or wet dentine loses on drying at 212° F. about 10 or 11 per cent. of free water; the dried dentine, when ignited at bright red heat, loses by decomposition of the hydrated salts 8 per cent. more water. The composition of dentine is therefore :

Fresh human dentine,—

Free water (which can be dried out at 212° F.)	10·0
Dry dentine	90·0
	100·0

And of dried human dentine,—

Organic matter	19·6
Combined water	8·4
Salts	72·0
	100·0

The proportion of salts to organic matter varies widely in different dentines ; thus elephant ivory (of the tusks) consists of—

Organic matter	34·0
Combined water	8·5
Salts	57·5
	100·0

Whilst the dentine of an elephant's molar contains a proportion of salts nearer to that of man—

Organic matter	21·0
Combined water	9·0
Salts	70·0
	100·0

Subject to the above correction, the following may be accepted as giving the constitution of dentine.

Von Bibra (2) gives the following analysis of perfectly dried dentine :

Organic matter (tooth cartilage)	27·61
Fat	0·40
Calcium phosphate, and fluoride	66·72
Calcium carbonate	3·36
Magnesium phosphate	1·08
Other salts	0·83

Von Bibra gives another analysis :

Cartilage	20·42
Fat	0·58
Salts	1·00
Magnesium phosphate	2·49
Calcium phosphate, and fluoride	67·54
Calcium carbonate	7·97

And Berzelius (¹) gives:

Gelatine and water	28·00
Sodium salts	1·50
Magnesium phosphate	1·00
Calcium phosphate	62·00
Calcium fluoride	2·00
Calcium carbonate	5·50

Gallippe (⁶) gives:

Water and organic matter	25·29
Mineral matter, consisting of—	
Soluble ash (alkaline chlorides, and phosphates)	0·54
Calcium carbonate	0·35
Magnesium carbonate	1·13
Calcium	45·11
Magnesium	1·67
Phosphoric acid	23·70
Silicates	0·41
Undetermined	1·8

The dentine of many mammals is very much richer in magnesium phosphate than human dentine. Even the latter, it would seem, from the discrepancies existing between the various analyses, is variable in composition; but, on the whole, it may be said that, amongst inorganic constituents of dentine, calcium phosphate largely preponderates; from 3·5 to 8 per cent. consists of calcium carbonate; a much smaller proportion consists of magnesium phosphate, while calcium fluoride exists in traces only.

Great discrepancies exist in the amount of carbonates estimated, and this arises from the great practical difficulty in making a quantitative analysis of small proportions of carbonic acid in a substance of which only very small quantities are obtainable, sources of error, which cannot be eliminated, thus creeping in.

It was the opinion of Hoppe-Seyler that the salt which chiefly hardens bone, dentine and enamel is a double salt, a compound of three equivalents of calcium phosphate with one of calcium carbonate, comparable to the mineral apatite.

Bone salt, $Ca_9\,(PO_4)_6$, $Ca\,CO_3$ or $Ca_{10}\,CO_3\,(PO_4)_6$.
Apatite, $Ca_{10}\,Fl_2\,(PO_4)_6$.
A variety of apatite, $Ca_{10}\,Cl_2\,(PO_4)_6$.

For a discussion of the probabilities of this being the case the reader is referred to Haliburton's "Physiological Chemistry," and to papers by the author in "Journal of Physiology," 1896 (²¹), and "Trans. Odontol. Soc.," 1896 (²²). The researches of Black (³), which have been in the main confirmed by independent analyses, and of Gallippe (⁶), indicate that the differences in the percentages of calcium salts in various human teeth have been over-estimated, and that there is but a very small range between the most perfect and the most frail teeth. But it is remarkable that the dentine of molars contains a slightly higher percentage of salts than that of incisors, the former containing 2 per cent. more ; this was indicated by the specific gravity experiments of Gallippe and subsequently confirmed by the author's analyses ([21]). Of the chemical constitution of the dentinal fibrils themselves little is known, except that they have been supposed not to consist of albumen, for, on treating pulverised dentine with salt solution rendered alkaline with sodic carbonate, only ·1 to ·75 per cent. of albumen was extracted ([26]) by two independent investigators. Still, this is not conclusive, as the comparative areas of the dentinal tubes and the solid matrix, as well as their respective specific gravities, are not known.

In the matrix of human dentine there is, under ordinary circumstances, little, if any, structure to be made out ; but the investigations of Howard Mummery have shown that in caries of the teeth, which are then to some extent decalcified, an appearance like connective tissue fibres can be seen in the matrix, and indications of the same thing can also be detected in some normal dentine.

This observation, which accords with the descriptions by von Ebner of a similar connective tissue in the matrix of bone and of dentine, is strongly confirmed by what obtains in some vaso-dentines. In this tissue the absence of a fine tube system renders it much more easy to see the nature of the matrix, which, under the influence of weak decalcifying agents, sometimes splits up into parallel fibres corresponding exactly in size and direction to the bundles of connective tissue fibrils which occur with complete regularity on the surface of the pulp.

Of the matrix of hard tubular dentine, then, it may be said that there is normally no visible structure, but that it sometimes breaks up in such a manner as to indicate that there really is some trace left of connective tissue fibres which were once present.

The action of acids in decalcification tends to soften and make the connective tissues generally swell up and become less visible, hence the difficulty of establishing their presence.

The Dentinal Tubes.—As has been already mentioned, the matrix is everywhere permeated by tubes, the precise direction of which varies in different parts of the tooth, so that the following description of their course must be taken as merely in a general way descriptive, and not as of universal or precise application.

Each tube starts by an open circular mouth upon the surface of the pulp cavity ; thence it runs outwards, in a direction generally perpendicular to the surface, towards the periphery of the dentine, which, however, it does not reach, as it becomes smaller, and divides into branches at a little distance beneath the surface of the dentine.

Near to the pulp they are so closely packed that there is little room between them for the matrix, while near to the outside of the tooth they are more widely separated; their diameter is also greater near to the pulp cavity.

The dentinal tubes do not pursue a perfectly straight course, but describe curves both on a larger and a smaller scale. The longer curves are less abrupt than the others, and are termed the "primary curvatures." They are often compared to the letter *f*, to which they bear a certain amount of resemblance, and are more pronounced in the crown than in the root.

The secondary curvatures are very much more numerous and are smaller. The actual course of the dentinal tube is, in most places at all events, an elongated spiral, as may be very well seen in thick sections transverse to the tubes; by alterations in the focus of the high-power objective of the microscope the appearance of the tube making a spiral turn is very striking. The effect of an elongated spiral viewed on its side will of course be only slight undulations, such as are the secondary curvatures of the tubes. The spiral course of the dentinal tubes is most strongly marked in the roots of teeth.

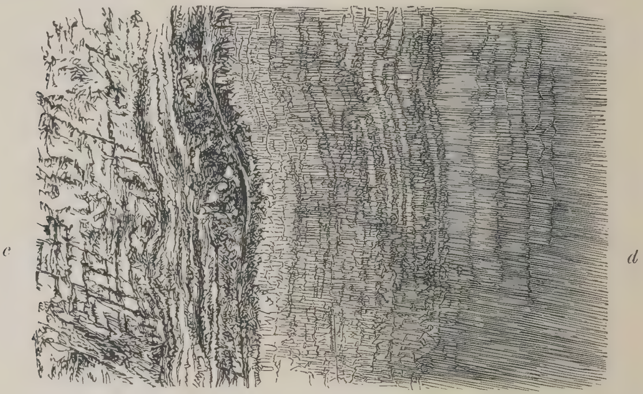

FIG. 46.—Dentine (*d*) and cementum (*c*) of the narwhal, showing contour lines due to rows of interglobular spaces.

When a transverse section of dentine is viewed, bands or rings, concentric with the pulp cavity, are seen, and the same bands may be seen in longitudinal section. Such a striated or laminated appearance in the dentine may be due to two causes, owing to its double origin not having always been kept in view, and some little confusion has arisen in the nomenclature. Such striæ may be due to the presence of rows of interglobular spaces, or to the coincidence of the primary curvatures of neighbouring dentinal tubes; that is to say, each tube bends at the same distance from the surface, and the bend makes a difference in the optical properties of the dentine at that point.

Schreger described these latter: "the lines of Schreger," therefore, are markings, ranged parallel with the exterior of the dentine, and are due to the curvatures of the dentinal tubes.

The "contour lines" of Owen, even in his own works, include markings of both classes: *i.e.*, those due to the curvature of the dentinal tubes, and those due to laminæ of interglobular spaces such as are met with in the teeth of *Cetacea*. Retzius had seen and described contour markings due to interglobular spaces, though his name is not usually associated with them.

Passing outwards, the tubes often divide into two equally large branches; they also give off fine branches, which anastomose with those of neighbouring tubes. In the crown of a human tooth these fine branches are comparatively few, until the tube has reached nearly to the enamel, but in the root they are so numerous as to afford a ready means of distinguishing whence the section has been taken. Mummery, using the silver-pyridin method of staining, has demonstrated very clearly these small branches. They are given off at right angles to the course of the main tube, which, however, itself frequently divides and subdivides, its divisions pursuing a nearly parallel course.

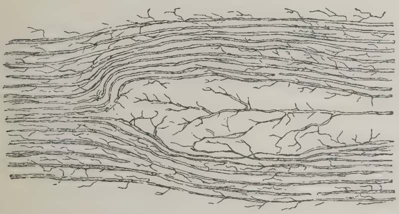

FIG. 47.—Termination of a dentinal tube in the midst of human dentine.

The tubes are subject to slight varicosities, and their course is sometimes apparently interrupted by a small interglobular space, as is to be seen in an extreme degree in the dentine of the *Cetacea*.

Owing to their breaking up into minute branches, some of the tubes become lost as they approach the surface of the dentine, and apparently end in fine pointed extremities.

Some terminate by anastomosing with terminal branches of others, forming loops near to the surface of the dentine; others terminate far beneath the surface in a similar way.

Some tubes pass into the small interglobular spaces which constitute the "granular layer" described by Sir John Tomes, while others again pass out altogether beyond the boundary of the dentine and anastomose with the canaliculi of the lacunæ in the cementum when they exist in that tissue.

The enamel also may be penetrated by the dentinal tubes when the latter enter enamel spindles, though this, when occurring in the human subject, must be regarded as almost pathological in its nature (see Figs. 34 and 48). As has, however, been mentioned in speaking of the enamel, in most of the marsupials, in a good many fish, *e.g.*, *Spherodus*, *Serrasalmo*, barbel, and in certain other animals, it is a perfectly normal and indeed characteristic occurrence, difficult though it be to see how such a relation of parts is brought about in the course of development of the two tissues.

Dentinal Sheaths.—If dentine be exposed to the action of strong acid for some days, a sort of fibrous felt, or if the action of the acid has gone further, a transparent slime, alone remains. Examined with the microscope, this proves to be a collection of tubes; it seems to be, in fact, made up of the immediate walls of the dentinal tubes, the intervening matrix having been wholly destroyed. Hamazawa (⁷), however, denies that the wall of the tubule is resistant to acid *; indeed, he goes so far as to deny the existence of a separate lining to the tubules (*i.e.*, Neumann's sheath). The structure so described by other writers Hamazawa regards as a prolongation of the cell membrane of the odontoblast carried into the tubule by the dentinal fibril.

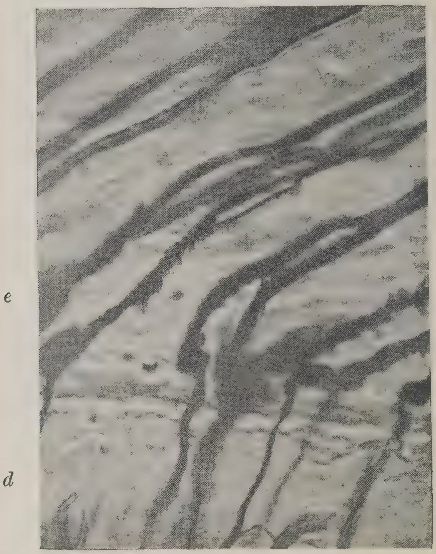

FIG. 48.—Enamel of Macropus: tubes at enamel margin. Fuchsin injected preparation. × 700. *d.* Dentine. *e.* Enamel. (Microphotograph by Mummery.)

Two facts are thus demonstrated: the one that the tubes have definite walls, and are not simple channels in the matrix; the other, that these walls are composed of something singularly indestructible. Indeed, the walls of the dentinal tubes are so indestructible that they may be demonstrated in fossil teeth, in teeth boiled in caustic alkalies, or in teeth which have been allowed to putrefy.

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* Hamazawa's views should be accepted with reserve, in view of the mass of evidence to the contrary.—ED.

Although Kölliker was, perhaps, the first to describe and figure these isolated tubes, they are generally known as the "dentinal sheaths of Neumann," the latter writer having more fully investigated and described them. The precise chemical nature of these sheaths will be more conveniently considered under the head of calcification; similarly indestructible tissues are, however, to be met with surrounding the Haversian canals and the lacunæ of bone.

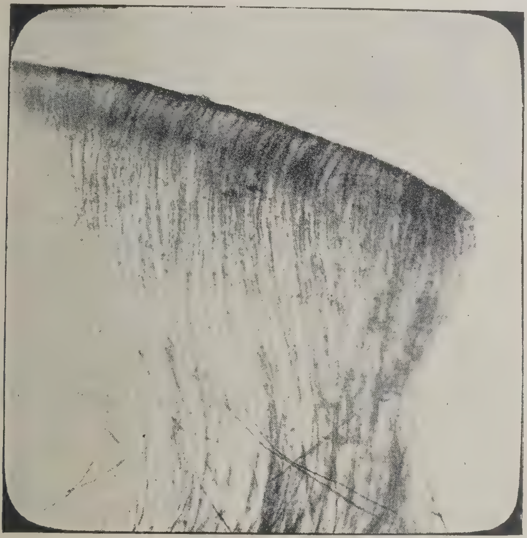

FIG. 49.—Ground section of human dentine, which has been submitted to the action of strong acids so as to isolate Neumann's sheaths by the destruction of the intervening matrix.

It was the opinion of Neumann, as it was also of Henle, that the dentinal sheaths are calcified; but the proof of this is very difficult, as they cannot be demonstrated, or isolated, to any extent in dentine, unless it has been decalcified. Their existence as distinct from the fibrils has been denied by Magitot, Sudduth, Römer, and more recently by Hamazawa (7).

Transverse sections of dentine present fallacious appearances, owing to the thickness of the section giving to the tube a double contour which may be easily mistaken for a special wall. Immediately round the opening of the canal, or "lumen," as it is called, there is, however, generally a thin yellowish border, which may perhaps be the sheath of Neumann. In the earlier stages of caries, before the dentine is much softened, the walls of the canals become strikingly apparent. But it must be remembered that the dentinal sheaths can only be fully demonstrated by processes which amount to a partial destruction of the dentine, and that they are therefore in some degree at all events artificial; it may be that they have no real existence until they are displayed more clearly by the action of these agents. If that is so, the immediate surroundings of the soft fibril differ somewhat in chemical constitution from the parts of the matrix which are more remote, so that under the action of destructive agents the matrix is split up into the sheathing layers round the fibrils and the more soluble residuum of the matrix.

Röse has succeeded, by Golgi's rapid method of nitrate of silver staining, in rendering Neumann's sheaths perfectly black, a transverse section of dentine thus prepared reminding one of the familiar tobacco-pipe appearance of dental caries, only that the sections of tobacco pipe are black. As the intervening matrix remains unstained, it is clear that Neumann's sheaths differ from it in the degree of calcification, an interpretation which is borne out by the fact that in a longitudinal section the youngest dentine layer so stained is also intensely black.

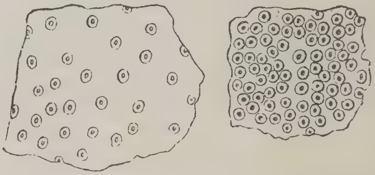

Fig. 50.—Transverse section of dentine. The appearance of a double contour is so much exaggerated as to make the figure diagrammatic, but it fairly represents the contour shown by nigrosin staining.

If, prior to treatment by Golgi's stain, the tooth be prepared by the Koch-Weil method, the soft parts, including the dentinal fibres, do not take the stain, so that in the transverse section the fibril is seen as a bright point in the middle of the black Neumann's sheath. In longitudinal section the black sheath is fringed all along the course of the tubes by processes more or less bridging across to the next ones, but the dentinal fibrils have not been demonstrated in these branches.

Röse concurs in describing Neumann's sheaths as especially resistant to acids and also to caries; hence the distinctness of the "tobacco-pipe appearance."

The author has succeeded in satisfactorily staining them by means of nigrosin; a preparation so treated would resemble Fig. 50, save that the opening of the tube would be light, and be surrounded by an intensely black border in place of the light one of the figure.

Dentine would thus be considered as a tissue made up of a calcified matrix, resembling that of bone, permeated by the soft fibrils, just as bone is permeated by canaliculi with soft contents, but having this peculiarity, that the latest formed portions of matrix, namely, those immediately embracing the fibrils, differ sufficiently from the bulk of the matrix in chemical constitution to enable them to be isolated as sheathing tubes, or to be stained *in situ*.

Dentinal Fibrils.—The canals which everywhere permeate the dentine are not empty, a fact which might be inferred from the difference in translucency and general aspect of dry and fresh dentine, whether seen in mass or in thin section; neither are they, as was at one time supposed, tenanted merely by fluid. This is well seen in the accompanying figure (Fig. 51).

Each canal is occupied by a soft fibril, which is continuous with a cell upon the surface of the pulp (odontoblast); the existence of these soft fibrils was first demonstrated by Sir John Tomes, who thus, to use the words of Waldeyer, "opened the way to a correct interpretation of the nature of the dentine."

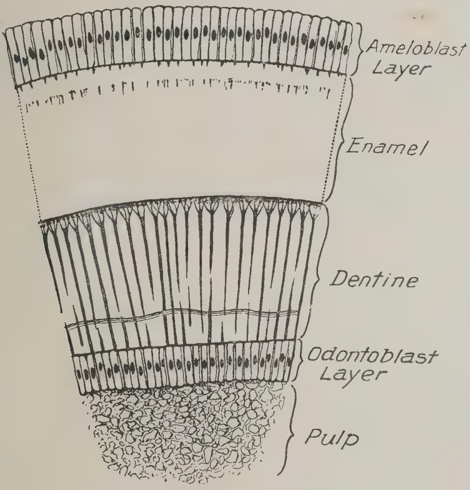

Fig. 51.—Transverse section through the tooth of a hedgehog stained with gold chloride. Semi-diagrammatic (Marett Tims).

Henle, in his "Allgemeine Anatomie" (1841), a translation of a portion of which is to be found in the "Archives of Dentistry" (1865), figured and described projections from dentinal tubes. These he described as calcified and rigid, adding that by the use of acids they may be made flexible; he speaks of the tube as empty, save when blocked by granular calcareous matter, and alludes to fluids entering it by capillarity; and, lastly, he says nothing whatever of the connections of the pulp with the tubes.

Müller (as translated in Nasmyth on the "Structure of the Teeth," 1839) says, "In breaking fine sections of the teeth perpendicularly to the fibres, I have frequently seen the latter projecting a little at the fractured edge. In such cases they are quite straight and not curved, and seem to be not at all flexible. Hence it follows that the tubes have an organised basis, a membrane, and that this is stiff and brittle, and probably saturated with calcareous salts, but weak and soft in a decalcified tooth."

The whole importance of Sir John Tomes' discovery lay in the fact that dentine is permeated by *soft, uncalcified structures;* and what is yet more significant, that these soft fibrils, permeating the hard dentine, proceed from the pulp. In no sense, therefore, did Henle anticipate this discovery.

In 1854 Lent figured processes from the odontoblasts which he conceived to be concerned in the formation of dentine; but in the earlier editions of the "Histology" of his friend and teacher, Professor Kölliker, although Lent's discoveries are described and adopted without reservation, no mention of the real structure of dentine occurs. In a later edition, however, Professor Kölliker says, "After Tomes had described a soft fibre in each tube, I fell into the mistake of supposing that these fibres and the tubes were one and the same."

The circumstances under which the dentinal fibrils can or cannot be discovered are said to be as follows, and may be taken as indications of a distinction between the dentinal fibrils and the dentinal sheaths:—

If a tooth section be submitted to the action of a caustic alkali and boiled in it, or be allowed to putrefy completely, so that the soft parts are entirely destroyed, the dentinal sheaths can still be demonstrated, but the fibres can in no way be brought into view (Kölliker). The dentinal sheaths may be demonstrated also in fossil teeth, as has been shown by Hoppe ([11]) and others.

In fresh dentine every odontoblast sends a process into the dentinal tubes (Tomes, Kölliker, Lent, Waldeyer, Neumann), and it has been found possible to demonstrate both the sheaths and the fibres in the same sections (Neumann, Boll).

In transverse and even in longitudinal sections of decalcified dentine the fibrils may be recognised *in situ* (Kölliker).

The contrast between the dentinal sheaths and the fibrils is this:— The sheaths are very indestructible, and can be demonstrated in teeth which have undergone all sorts of change; the soft fibril is no longer demonstrable when the tooth has been placed in circumstances which would lead to its soft parts perishing. In dentine, then, there exist (i.) a matrix permeated by canals; (ii.) soft fibrils contained in these canals, or "dentinal fibres"; and probably also (iii.) special walls to these canals, or "dentinal sheaths"; and it now remains to consider these in further detail.

In sections of small fragments of dentine taken from the edges of the pulp cavity and including the surface of the pulp, the dentinal fibrils may be seen stretching from the cells of the superficial layer of the pulp (odontoblasts) into the dentinal tubes, as, owing to their being extensile, they may be stretched or drawn out from the tubes for some little distance without being broken across. In the same way they may be seen stretching across like harpstrings between two pieces of dentine when this is torn by needles, and they can be thus shown in fresh fragments just as well as in those of decalcified dentine. When stretched to a considerable extent their diameter becomes diminished and they finally break, a sort of bead sometimes appearing at the broken end (J. Tomes). This would seem to indicate that the substance of the fibril is of colloid consistency, and that its external portions are in some degree firmer than its axial portion.

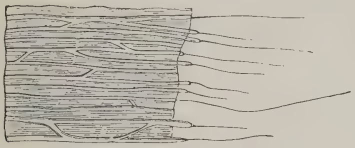

FIG. 52.—Section of dentine from the edge of which hang out the dentinal sheaths, and beyond these again the fibrils. (After Boll.)

The dentinal fibrils are well seen in Figs. 51 and 53, in which many are attached to the odontoblast cells.

Modern methods of histological research have made the demonstration of the fibrils, which are continued from the odontoblast cells and enter the dentinal tubes, an easy matter; they are of some size, and, judging from appearances, are pretty firm in consistence, as they look somewhat stiff where they are seen projecting from the surface of a torn-away pulp.

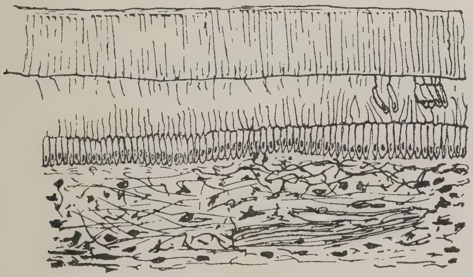

FIG. 53.—Surface of the pulp with the odontoblast layer *in situ*. The dentine fibrils pulled out of the dentinal tubules hang like a fringe from the odontoblast layer; dentine fibrils are also seen hanging out from the edge of the dentine, to which, to the right of the figure, a few odontoblasts remain attached.

They stain very readily with hæmatoxylene, gold chloride, &c., and many other stains are slightly taken by them. Another easy method of staining the fibrils is to treat the pulp with a salt of iron followed by tannin, of course after a thorough washing.

The dentinal fibril is capable of being stained with carmine; in young dentine it is more easily stained, especially near the pulp cavity, and the following figure (Fig. 54) is taken from such a section of dentine from a partially-developed human incisor. The matrix is slightly stained with the carmine, indicating that it has not yet become fully impregnated with salts, and in the centres of the clear areas, dark spots deeply stained with carmine are to be seen, the latter being transverse sections of the dentinal fibrils *in situ*. The author has observed precisely similar appearances in the thin young dentine of calves' and pigs' teeth; Kölliker also mentions that the dentinal fibril may be recognised *in situ* in transverse sections of fresh dentine.

Bödecker finds that the dentinal fibrils stained darkly with chloride of gold, when viewed in transverse sections under a magnifying power of 2,000 diameters, do not appear round but somewhat angular, and give off tiny lateral offshoots which seem to penetrate the dentine (see Fig. 54). In the matrix itself there is an appearance of a faint network when it has been stained with gold, and from this Bödecker infers, though probably erroneously, that the dentine is penetrated everywhere by a network of living plasm, derived from, though far finer than, the dentinal fibrils. (Cf. results of Golgi's stain, p. 80.)

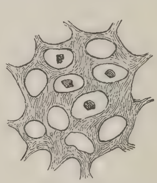

Fig. 54.—Transverse section of dentine; in four of the dentinal tubes, the dentinal fibrils, deeply stained with carmine, in the preparation from which this figure was drawn, are seen. The fibrils are somewhat shrunken, owing to the action of the glycerine in which the section is mounted.

Probably the angularity of the fibril, which, as figured by him, is much smaller than the canal, is due to its having shrunk under the action of chromic acid or some such reagent.

According to Neumann, in old age the fibrils atrophy or become calcified; some observers have failed to detect them near to the periphery of the dentine, far away from the pulp cavity. But here they would naturally be more minute, and it is more probable that the manipulations had failed to demonstrate them than that they were absent, for Bödecker has traced them to the very periphery of the dentine.

Dr. Beale has seen prolongations of the nucleus of the cell towards the base of the fibril, though in the example which he figures it does not enter it.

Dentinal fibrils were demonstrated in the *Reptilia* and *Amphibia* by Santi Sirena and by the author, and also by the latter in the few fish examined with that purpose.

Of their real nature some doubts are entertained; they are certainly processes of the odontoblasts, and their substance seems identical with that of the protoplasm of the cell, for they are of tolerably large size, and are larger at their origin than at their terminations. According to Hopewell-Smith (9), the odontoblasts vary considerably in size, those in the coronal part of the pulp of a fully grown tooth measuring 25μ to 30μ in length, and about 5μ in breadth.

[Hopewell-Smith has suggested that the odontoblasts partake of the nature of nerve-end organs, but such an interpretation is doubtful on embryological grounds, and also from the statement made by several observers that the nerve fibres of the pulp enter the dentinal tubules independently of the odontoblasts.]

Coleman once suggested that it was possible that the odontoblasts might have some tactile function, and Hopewell-Smith (10) points out their resemblance to multipolar ganglion cells of the spinal cord. According to Magitot, the nerves of the pulp become continuous with a layer of reticulate cells which lie beneath the odontoblasts; these communicate freely with the processes of the odontoblasts, so that there is a very direct chain of communication between the dentinal fibril and the nerves of the pulp. Magitot speaks very positively as to the accuracy of his views, which as yet, however, have not been confirmed by other investigators (Fig. 55).*

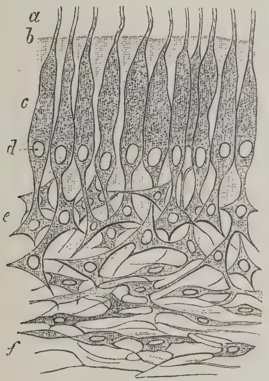

FIG. 55.—*a.* Dentinal fibrils. *b.* Amorphous matrix. *c.* Odontoblasts. *d.* Nuclei of odontoblasts. *e.* Stellate cells. *f.* Nerve extremities which are continuous with the branched cells. (After Magitot.)

Yet another view of the nature of the dentinal fibril is advocated by Klein (12) (p. 187), who holds that the odontoblasts are concerned only in the formation of the dentine matrix, and that the dentinal fibrils are long processes of the deeper cells in the above figure, which run up between the odontoblasts and enter the dentinal canals.

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* The objection has been urged against the view that the prolongations from the odontoblasts into the dentinal tubules (the dentinal fibrils) have any sensory, *i.e.*, nervous, function, on the ground that the odontoblasts are of mesoblastic origin, whereas the nervous system as a whole is derived from epiblast. There is, however, a tendency at the present time amongst some embryologists to lay less stress than formerly on the germ-layer theory. It is therefore conceivable that in future this objection may lose some of its force.—ED.

In a later paper (¹³) Magitot also impugns the accuracy of the views ordinarily accepted as to the structure of dentine, denying the existence of any special walls to the tubes, and further arguing that it is undesirable to think or speak of the channels in dried dentine as tubes at all. For, he argues, they are not tubes in the fresh state, seeing that the fibrils are adherent to the matrix and form a part of it, and that they were originally precisely the same tissue. He would prefer to speak of dentine as being a fibrillar tissue included in a hard and homogeneous matrix.

In this opinion Magitot does not stand alone: Xavier Sudduth does not believe in the existence of a specialised sheath, and Römer (¹⁷) also holds strongly that the processes of the odontoblasts constitute the whole contents of the dentinal tubes, *i.e.*, that they lie in canals in the dentine matrix, which have no special walls. According to him, therefore, the residue left after the destruction of the matrix by strong acids (Fig. 50) consists of the processes of the odontoblasts, and of these alone.

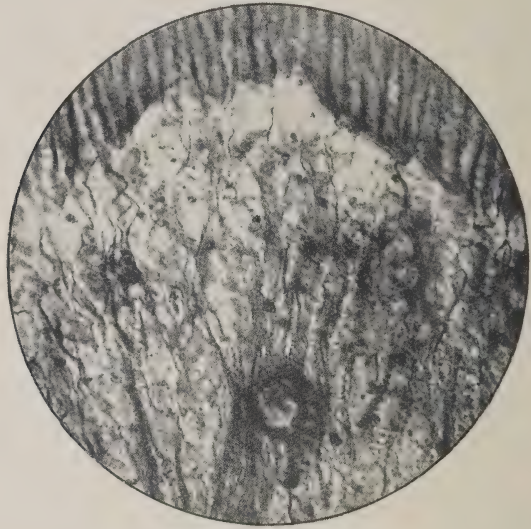

Fig. 56.—Section showing non-medullated nerve fibres passing from the pulp between the odontoblasts and entering the dentinal tubules. (From Mummery's paper from British Dental Journal, October 1, 1913.)

These views, however, do not differ substantially from those in the text, save that Magitot does not recognise the existence of that transitional tissue which others believe to be there, and call the sheaths of Neumann.

The balance of evidence is against this view of Magitot and Sudduth. If they were right one would have the anomaly of sensation being conducted by a material so indestructible by acids as to have departed far from the protoplasmic condition which is associated with functional activity, unless the penetration of actual nerve fibres be admitted.

Both Morgernstern and Römer believe that non-medullated nerve fibres pass from the pulp into the dentinal tubes, and end in the "enamel spindles," and Howard Mummery (13) is of the opinion that, as they approach the plexus of Raschkow, the nerves of the pulp, passing between and around the odontoblasts, form a narrow marginal plexus from which they extend, as non-medullated fibres, into the dentinal tubes, and accompany the dentinal fibrils to their terminations beneath the enamel or cementum (Fig. 56). The observations of Mummery appear to receive confirmation in a paper by Deppendorf (5) and others.

Mummery's iron preparations clearly show that fine fibres traceable into connection with indisputable nerve bundles deeper in the pulp do run out straight towards the dentine and right up to it as though they entered it, which, perhaps, they do.

In this connection the very remarkable specimens of Dr. Dentz, of Utrecht, may be mentioned. These, which were cut from embryos when about half the thickness of the dentine was formed, show pear-shaped bodies arranged with regularity a short distance within the border of the dentine, the smaller ends being directed towards the pulp, and their large ends connected with one or more dentinal tubes. These pear-shaped bodies have two or three large nuclei, and present a close resemblance to some forms of nerve-end organs.

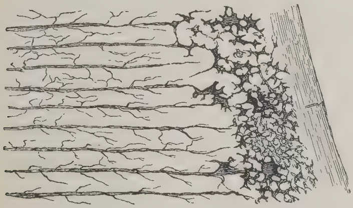

Fig. 57.—Dentinal tubes terminating in the spaces of the granular layer.

Amongst many difficulties as to their interpretation is the fact that the examination of a large number of sections of dry deciduous teeth has quite failed to reveal the spaces which might have been expected to have contained them, and their relatively large size ($\frac{1}{400}$ of an inch) would render the spaces conspicuous.

The observation of Boll is also very suggestive. He found that by treating a perfectly fresh pulp with $\frac{1}{8}$ per cent. solution of chromic acid an immense number of fine fibres could be demonstrated, a great many of which projected from above the surface, as though they had been pulled out of the dentinal tubes, but although they pass up from a plexus of dark-bordered nerve fibres beneath the membrana eboris between the cells of that layer, their passage into the dentine remains a mere matter of inference.

There can be no question that the sensitiveness of the dentine is due to the presence of soft organised tissue in the tubes, and is not a mere transmission of vibrations to the pulp through a fluid or other inert conductor. The peripheral sensitiveness of a tooth can be allayed by local applications which it would be absurd to suppose were themselves conducted to the pulp; moreover, it is within the experience of every operator that after the removal of a very sensitive layer of caries an area of dentine is reached, which, though nearer to the pulp, is far less sensitive, a condition quite inexplicable, except upon the supposition of a different local condition of the contents of the tubes.

With reference to the probabilities of actual nerve fibres entering the dentinal tubes, it must be remembered that, in those tissues which are naturally so thin as to present great facilities for examination, nerves of a degree of fineness unknown elsewhere have been demonstrated; in other words, the easier the tissue is to investigate, the finer the nerves which have been seen in it, while dentine is among the most difficult substances conceivable for the demonstration of fine nerve fibrils.

[In view of the many diverse and often conflicting statements made by competent observers, the question as to the precise mode by which the dentine is innervated must be regarded as still *sub judice.*]

Interglobular Spaces.—In the dentine which underlies the cementum, though often separated from the latter by a clear structureless layer, an immense number of these spaces exist, giving to the tissue, as seen under a low power, an appearance of granularity and constituting the "granular layer" of Sir John Tomes. On account of the greater abundance of these spaces in that situation, they are more evident beneath the cement than beneath the enamel, and many of the dentinal tubes appear to terminate in them (Fig. 57).

Hopewell-Smith appears to regard each granule as a sort of compromise between an interglobular space and a lacuna of pathological cementum; he points out that, though the term "granular layer" obviously applies to the spaces, the layer is really situated in a matrix of dentine which is distinctly granular.

Although the name "interglobular spaces" is strictly applicable to the structures constituting the granular layer of dentine, it was not to these that it was first applied. When a dried section of dentine is examined, dark irregular spaces clustered together, and usually most abundant at a little distance below the enamel, are often to be seen, particularly if the section has been made from a brownish, imperfectly developed tooth.

The spaces have a rounded outline, furnished with short pointed processes, and in favourably prepared sections it may be seen that their outlines are formed by portions of the surfaces of closely apposed spheres, and globular contours may often be detected in the solid dentine near to them, as is shown in Fig. 58, taken from a section boiled in wax in order to render it very transparent.

Although these large spaces are very common, they are not universally present, or at any rate they cannot always be demonstrated. They are perhaps not to be regarded as perfectly normal, but are rather indications of an arrested development at that spot. The occurrence of globular forms during the early stages of calcification will again be alluded to in connection with the development of teeth; but although the term "interglobular" is thus strictly applicable, the use of the word "spaces" is not so correct. In dry dentine it is true that they are, as Czermak described them, spaces filled with air; but that they are so is only due to the fact that their contents are soft, and shrivel up in drying. In the fresh condition the interglobular "space" is perfectly full, its contents often having the structural arrangement of the rest of the matrix, or else consisting of soft plasm; in the former case, the dentinal tubes pass across and through it without any interruption or alteration in their course. This fact, as well as the softer nature of the contents as compared with the rest of the dentine, is well illustrated by a section in the author's possession which was taken from a carious tooth, near to the affected surface. In this the bacteria had effected an entrance into some of the tubes, giving to them a varicose or beaded appearance, and causing their enlargement. But when the micro-organisms reached the interglobular space, the less amount of resistance, or possibly the more favourable pabulum accessible, led to their more rapid development, so that the tubes within the confines of the space are many times more enlarged than those outside; nevertheless the continuity of the tubes across the space is well demonstrated by the multiplication of micro-organisms having followed them with exactitude.

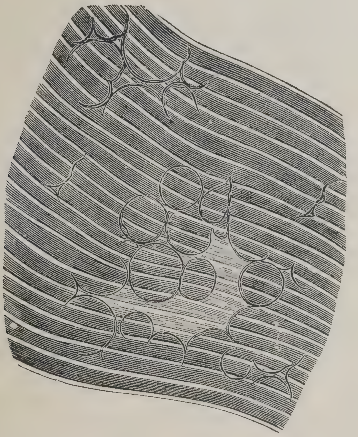

FIG. 58.—Interglobular spaces in dentine.

It sometimes happens that indications of spherical forms with faintly discernible contours resembling those of the interglobular spaces may be seen in dried sections, in which no actual spaces occur.

The appearances are perhaps produced by the formation of an interglobular space, the contents of which have subsequently become more or less perfectly calcified. The term "areolar dentine," formerly applied to this, is falling into disuse, although it can very well be applied to one form of adventitious dentine, the outcome of dental caries.

Globular forms, showing concentric lamination like an onion, are very distinct in the outer part of the dentine in some fossil reptiles (Credner, [4]).

The exact nature of the contents of the interglobular spaces is not very certain; they may easily be tinted by carmine, and it is said that they may, like the dentinal sheaths, be isolated by the destruction of the rest of the matrix in acids. Like Neumann's sheaths, they take a deep black stain with Golgi's process.

Bödecker says that there is soft living plasm abundantly distributed in the smaller interglobular spaces which constitute the granular layer, and that this is in very free communication with the soft fibrils in the tubes on the one side and with the soft contents of the lacunæ and canaliculi of the cementum on the other.

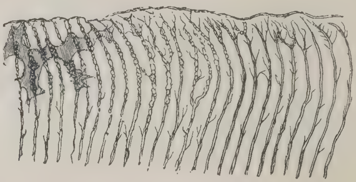

Fig. 59.—Section of carious dentine, in which some of the tubes are enlarged by the ingress of organisms, which have developed with greater freedom in one or two of the tubes where they cross the interglobular spaces.

Varieties.—In the dentine so far described, which is that variety known as hard or unvascular dentine (ortho-dentine), some degree of nutrition is perhaps provided for by the penetration of the whole thickness of the tissue by protoplasmic fibres, the dentinal fibrils; but this nutrition may be effected in a different way, and there are other varieties of dentine known in which dentinal fibrils have never been shown to exist. For descriptive purposes the author would classify dentines as:

(i.) Hard, unvascular, or ortho-dentine.
(ii.) Plici-dentine.
(iii.) Vaso-dentine.
(iv.) Osteo-dentine.

Another classification has been proposed by Röse, to which fuller reference will be made at a future page. He does not recognise plici-dentine as a variety, and proposes the term trabecular dentine instead of osteo-dentine (see p. 107).

Of these ordinary hard dentine has been sufficiently described.

Plici-dentine.—This is a variety of hard dentine, not very distinct in its essential nature, though at first sight widely dissimilar. In ordinary dentine the dentinal tubes radiate out from a pulp and pulp chamber of simple form. If that form is rendered complex by foldings of its walls, the dentinal tubes still running off at right angles to that portion of the pulp to which they immediately belong, a "plici-dentine" results. It is merely an ordinary dentine with its pulp folded up and wrinkled into a greater or less degree of complexity.

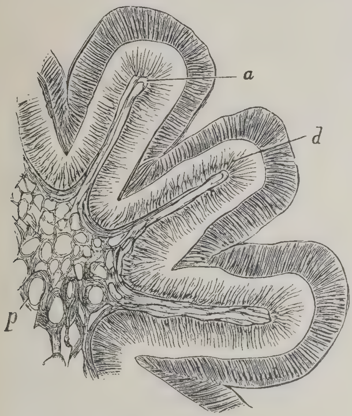

FIG. 60.—Section of plici-dentine with the pulp *in situ* (*Lepidosteus*). *a*. Prolongation of the pulp. *p*. Connective tissue framework of pulp. *d*. Dentine.

In the teeth of *Varanus* (monitor lizard), or of *Lepidosteus*, for example, the process of calcification of the pulp takes place in such manner that in the upper half of the tooth a cap of ordinary unvascular dentine, in which the tubes radiate from a single central pulp cavity, is formed. But in the lower part of the tooth slight longitudinal furrows appear on the surface, which, on transverse section,

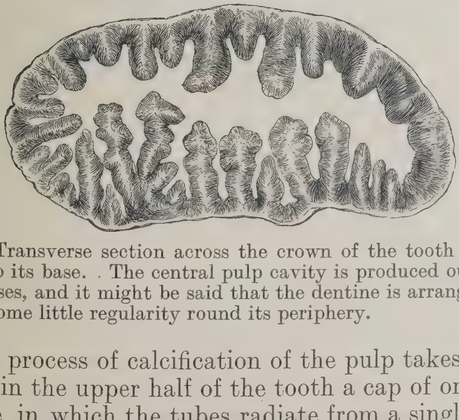

FIG. 61.—Transverse section across the crown of the tooth of *Varanus*, near to its base. The central pulp cavity is produced outwards into processes, and it might be said that the dentine is arranged in plates with some little regularity round its periphery.

are seen to correspond to involutions of the dentine; the dentine is, as it were, in folds. The pulp on section might be compared to a paddle-wheel, the floats on which correspond to the thin flat radiating processes of the pulp; but as yet the central axial pulp chamber is unaltered. In *Lepidosteus* (the North American gar-pike), a little lower down, as represented in Fig. 62, there is no longer a central simple pulp chamber; the inflections round the periphery have become relatively much deeper, and the centre of the tooth is occupied by a tissue irregular, but not otherwise unlike the dentine of *Myliobates* (cf. p. 95); that is to say, there are a number of columns of pulp, each of which forms an axis whence a system of dental tubes radiates.

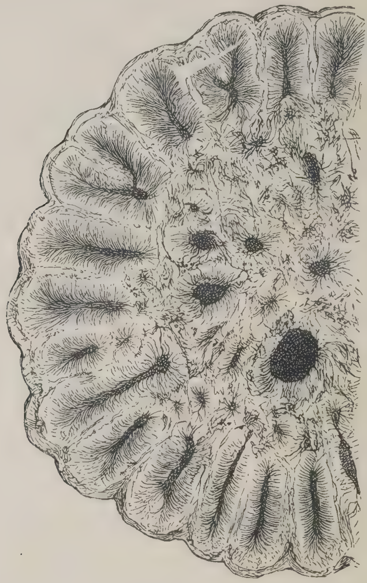

FIG. 62.—Transverse section across the base of a tooth of *Lepidosteus spatula.* At the exterior are regularly disposed radiating plates of dentine, each with its own pulp cavity, while the central area is composed of more or less cylindrical pulp chambers, each of which forms the starting point for its own system of dentinal tubes. The pulp chambers are made dark in the figure for the sake of greater distinctness.

The outrunning plates of dental pulp, which on section radiate out like the spokes of a wheel, do not always remain single; they may divide simply into two branches, as may be seen in the section across the base of the tooth of *Lepidosteus*, or sometimes there are several branches.

In *Lepidosteus oxyurus* there are simple inflections, and a central pulp cavity; in *L. spatula* the inflections are branched, and the central pulp cavity all filled up.

In the foregoing figure of the base of a tooth of *Lepidosteus* some few of the outrunning pulp chambers are seen to be bifurcated, while the central mass of the tooth is composed of dentine permeated by pulp canals which pursue a longitudinal course. A slight further modification leads up to the complicated structure of the dentine of *Labyrinthodon*, in which a maximum of complexity is attained, although the clue to its intimate structure is afforded by the teeth of *Varanus* or of *Lepidosteus*.

The laminæ of pulp, with their several systems of dentinal tubes, instead of passing out in straight lines like the spokes of a wheel, pursue a tortuous course as they run from the small central pulp chamber towards the surface. Not only do they undulate, but they also give off lateral processes; and at their terminations near to the surface of the tooth the thin laminæ of pulp (so thin that the radiating pulp chambers are mere fissures) become dilated; so that on section circular canals are seen at these points, as is also the case at the points where subsidiary processes branch off.

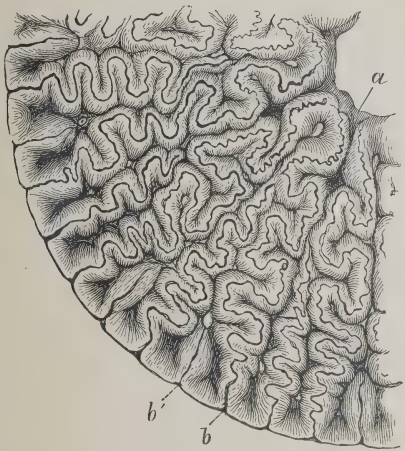

Fig. 63.—Transverse section of a tooth of *Labyrinthodon*. (After Owen.) The letter *a* is placed in the centre pulp chamber; the letter *b* marks the lines of separation between the systems of dentinal tubes which belong to each lamina of pulp; these lines of demarcation were formerly supposed to be occupied by cementum.

The wavy course pursued by the radiating plates of dentine, and the disposition of the tubes round the dilated portions of the pulp chamber, render the general aspect of the dentine structure very complicated; the several "systems"* are united to one another by an inosculation of the terminal branches of the tubes in some few places, but more generally by a clear layer containing radiate spaces, something like the lacunæ of cementum. Hence Professor Sir Richard Owen described the tooth as consisting of radiating plates of dentine, between which equally convoluted plates of cementum penetrate. But, as was pointed out by Sir John Tomes (^{20}), the mere presence of lacuna-like spaces is not sufficient to prove the presence of cementum, inasmuch as they occur on a small scale in the granular layer of dentine. Moreover, when cementum and enamel are both present, the cementum is always outside the enamel, whereas at the upper part of the tooth of the *Labyrinthodon* the characteristic inflections take place within a common investment of enamel which is not involuted. Thus the whole of the tissue constituting the very complex pattern of the *Labyrinthodon* tooth is dentine, and the cementum does not, as was usually supposed, enter into its composition at all.

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* The term "dentinal system" is applied to the portion of dentine in which all the tubes radiate from a single section of pulp chamber; thus the tooth of *Labyrinthodon* is made up of many dentinal systems; the same may be said of *Myliobates*.

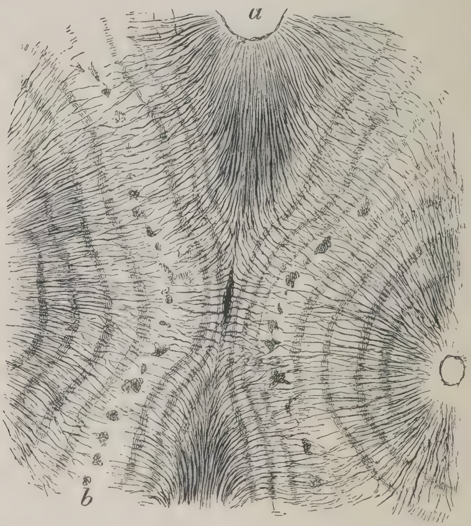

FIG. 64.—From tooth of *Labyrinthodon*, showing the nature of the connection between the contiguous dentinal systems. *a* and *b* as in previous figure. (After a drawing by Sir John Tomes.)

So far the foldings have been lateral, and in many cases the tip of the tooth was a simple cone without any foldings. There is another kind of dentine which has much in common with these plici-dentines, but which is a little more difficult to classify. This is found in the teeth of the Cape ant-eater (*Orycteropus*); in the teeth of *Myliobates*, a large ray; or in the teeth of the rostrum of the saw-fish (*Pristis*).

In the *Myliobates* (Fig. 65) the flat pavement-like tooth is permeated by a series of equidistant, parallel, straight canals, running up at right angles towards the surface, from the upper end and sides of which systems of dentinal tubes radiate, just as the tubes radiate from the single pulp chamber of a human tooth, save that they run for a comparatively short distance. In transverse sections the tubes are seen radiating from these canals, and at their terminations sometimes inosculating with the terminal branches of the tubes of another system. The channels contain prolongations of the vascular pulp, which are distinct in the upper part of the tooth, but become intimately united together at its base, where the disposition of the channels ceases to be regular, and, as a consequence,

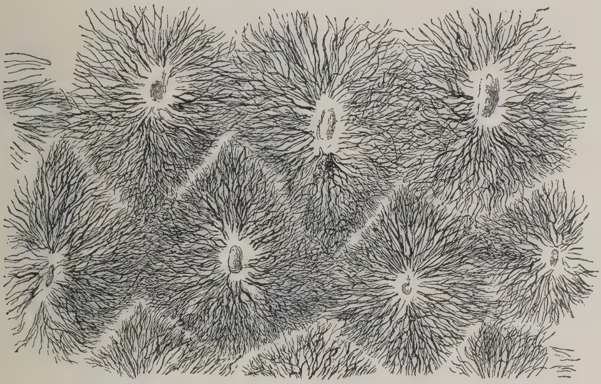

FIG. 65.—Transverse section of the dentine of *Myliobates.*

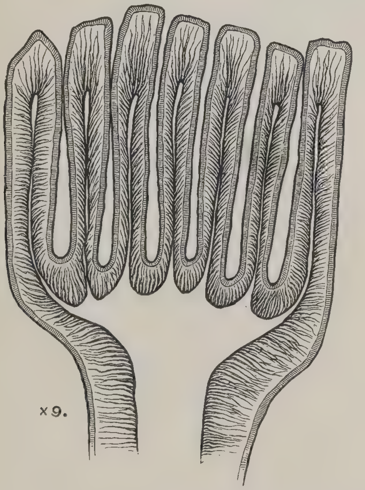

FIG. 66.—Longitudinal section of lower incisor of *Galeopithecus.*

the systems of dentinal tubes pass from them in various directions without producing the symmetrical patterns which characterise the upper part of the crown.

When the tooth comes into use and its immediate surface gets worn off, the ends of the perpendicular pulp canals would be laid open were it not that they become blocked by the deposition of a transparent homogeneous tissue within them, resembling the similar tissue which closes the Haversian canals of an antler about to be shed.

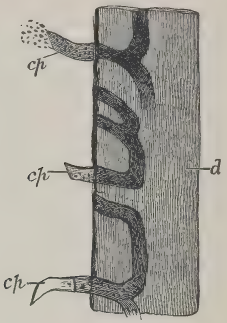

Fig. 67.—Section of dentine from a freshly caught hake. *d.* Dentine matrix. *cp.* Capillary channels with blood vessels hanging out from the edge, containing here and there abundant blood corpuscles.

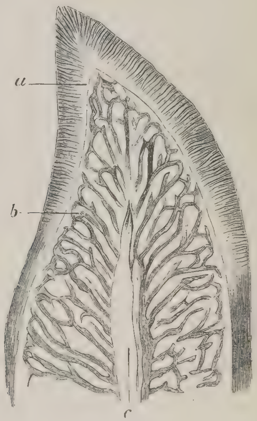

Fig. 68.—Tooth of *Ostracion*. *a.* Enamel. *b.* Capillary channels in the dentine. *c.* Pulp chamber.

Instead of being regarded as a plici-dentine, such a tooth might be said to be built up of a series of small, parallel, fused denticles, or exceedingly broadened and fused cusps. Without attaching too much weight to the comparison, if we imagine the comb-like tooth of *Galeopithecus*, a lemurine animal, to be devoid of enamel, and the cusps to be squeezed together into lateral contact, we should have a structure closely resembling a single row of the denticles of *Myliobates*.

The point which it is wished to emphasise is that the dentinal systems in the latter are of the ordinary type of a fine-tubed or ortho-dentine, and it is only in the manner of their aggregation that they come to present a very different-looking structure. Hence any classification which removed such a dentine far from an ortho-dentine would appear to be misleading. The arrangement of the tubes in *Pristis* is, however, a little different: they are fewer and are more branched, and do not fill up the periphery of each system so completely.

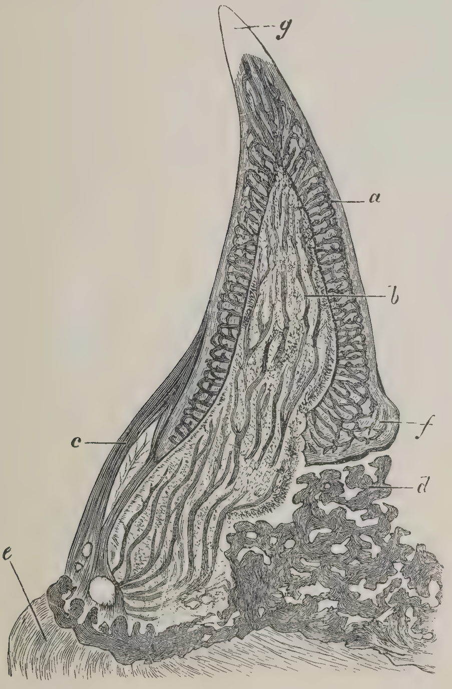

Fig. 69.—Hinged tooth of hake. *a*. Vaso-dentine. *b*. Pulp. *c*. Elastic hinge. *d*. Buttress of bone to receive *f*, formed out of bone of attachment. *e*. Bone of jaw. *f*. Thickened and rounded free base of tooth. *g*. Enamel tip.

Vaso-dentine.—In dentine, as so far described, the existence of a system of fine tubes—dentinal tubes—has been the most conspicuous feature, but there are tissues equally entitled to be called dentine in which no such tube system exists at all.

But, as it would seem necessary that some living material should permeate any tissue which is for any length of time to be retained in close connection with the rest of the organism, these dentines are not solid, but are permeated by a much larger tube system, the canals being in this case channels in which blood circulates through capillaries, so that during the life of the animal the teeth look quite pink, and in a section cut from the fresh tooth the coats of the capillary may be seen to hang out from the edge, and the vessels to be full of blood corpuscles (Fig. 67). The arrangement of the vascular canals is regular and striking, reminding one of the appearance of the vessels in an intestinal villus ; in fact, an intestinal villus petrified, whilst its capillary network remained pervious, and red blood continued to circulate through it, would form no bad representation of a typical vaso-dentine tooth.

In all the vaso-dentine teeth with which the author is acquainted, the pulp chamber is of simple form, so that the conical pulp can be pulled out, and no tissue, or next to none save the blood vessels, enters the canals, which are therefore of almost uniform diameter, and each capillary almost or quite fills and fits its canal.

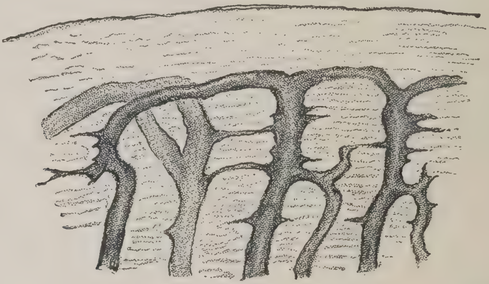

Fig. 70.—From the tooth of the hake. The thorn-like processes are seen, as also a faint lamination of the matrix.

The matrix does not present a very definite structure, though there is generally some appearance of lamination parallel with the surface, and what has just been said with reference to the canals requires modification in so far as there are, in dry specimens, slight narrow spaces, thorn-like in section, which run from the canals between the laminæ (Fig. 70).

These are not present in all vaso-dentines, but may be found in a good many, as, for example, in the hake, from which the figure has been drawn.

Röse describes the outer part of the hake's tooth, beyond the vascular loops, as vitro-dentine. But the author does not find that the dentine here differs either in the manner of its development or in its ultimate structure from the dentine which intervenes between the vascular loops, and hence to give it a distinctive name is unnecessary and misleading. The outer portion of a cod's tooth is more distinct in structure, but its character is not such as to lead one to apply the term vitro-dentine to it.

As a rule the vascular canals do not extend quite out to the surface, but terminate sometimes in a bounding canal, and sometimes without one, at a very definite distance within the surface (Fig. 71); this perhaps represents the original limit of the capillaries in the formative pulp. But however that may be, the structure of the matrix outside them is, in some examples, very interesting in view of recent investigations into the development of dentine.

This outer layer looks exactly like a calcified connective tissue which has preserved all its form, and it is not obscured by the occurrence in it of any tube system, interglobular spaces, or other structures.

Such in brief are the characters of a typical vaso-dentine, but there are vast numbers of forms of this tissue which serve to bridge over the gap which would seem to exist between it and hard dentine. Thus in the conical teeth of the flounder, and indeed of many flat fish (*Pleuronectidæ*), the tips of the teeth are composed of ordinary fine-tubed dentine, surmounted by enamel tips. In this part of the tooth the tubes radiate outwards in the ordinary way from the pulp chamber, and are both numerous and regular, but lower down in the tooth the dentinal tubes become less numerous, and *pari passu* with their diminution vascular canals begin to make their appearance, till, as the base of the tooth is reached, tolerably typical tubeless vaso-dentine is found.

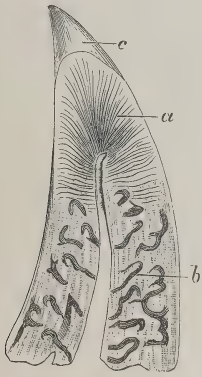

Fig. 71.—Tooth of flounder. *a.* Hard dentine. *b.* Vascular canals. *c.* Enamel tip. For other examples of vaso-dentine, see the figures of the teeth of *Chætodon* (Fig. 167, p. 266), of *Odontostomus* (Fig. 149, p. 233), &c.

It may be supposed, therefore, that the two sorts of tubes are capable of taking the place of one another, and that the nutrition of the dentine may be provided for either by protoplasmic material running for a long distance from the pulp through dentinal tubes, or by blood brought nearer to hand by the vessel-carrying canals, but that both are not required, and so do not co-exist in full development.

But from the flounder's tooth it may be learnt that hard dentine and vaso-dentine are not fundamentally dissimilar, and that they may pass into one another by imperceptible gradations, so that it cannot be said exactly at what point the name of vaso-dentine is to be given to it. And within the limits of a single family of fish—the *Gadidæ,* or cod-fish family—there are to be found all grades of vascularity, from the complete and regular system of vascular channels existing in the hake to the sparse canals of the haddock and the pollock; in *Lotella* there are neither dentinal tubes nor vascular canals, but a simple laminated structure.

Röse states that the very small teeth of young haddocks are without vascular canals, and calls them vitro-dentine, and also states that the small teeth of very young pike consist of normal dentine without an osteo-dentine (trabeculo-dentine) core. But size of teeth alone does not determine a departure from the normal type. Thus the tiny teeth in the gill arches ("gillrakers") of the hake consist of a beautiful vaso-dentine, whilst among the *Gadidæ* are fish with teeth of large size but only simple structure. (Cf. C. S. Tomes,[23].)

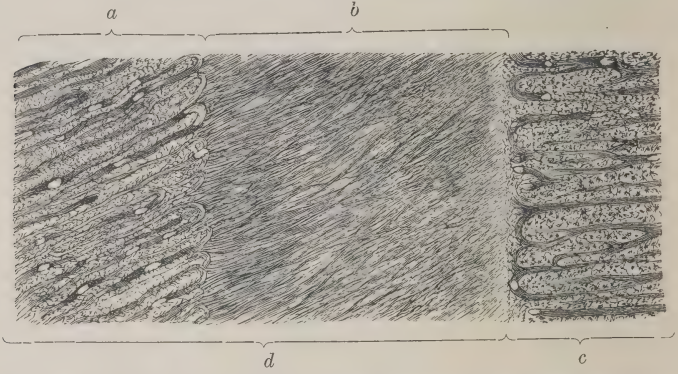

FIG. 72.—Dentine and cementum of *Megatherium;* the latter lies to the right. *a.* Vascular dentine. *b.* Fine-tubed dentine. *c.* Cementum. *d.* Dentine.

The great extinct *Megatherium* possessed a dentine which was very rich in vascular canals, but their arrangement was a little different from that just described, as may be seen in the figure (72) to the left of which lies the inner portion of the dentine, very rich in vascular canals; this merges into a fine-tubed dentine (*b*), the vascular canals all ending at the same distance from the surface, while outside this again comes the very vascular cementum (*c*).

Mummery describes vascular canals present in the dentine of *Sarcophilus ursinus* (Tasmanian Devil) and also in *Cynomys* (the Prairie Marmot). In the latter, he states that they were present "in great abundance."

The typical vaso-dentine teeth appear to be a good deal softer than those which are composed of fine-tubed dentine, and accordingly they are generally either completely coated, or at all events tipped, with enamel.

It occasionally occurs that a vascular canal persists in the hard dentine of a human tooth. In such cases there is no relation between these canals and the course of the dentinal tubes, the latter being (as is seen in Fig. 73, drawn from a specimen shown to the author by Dr. Andrews at Cambridge, Massachusetts) displaced from their course by it.

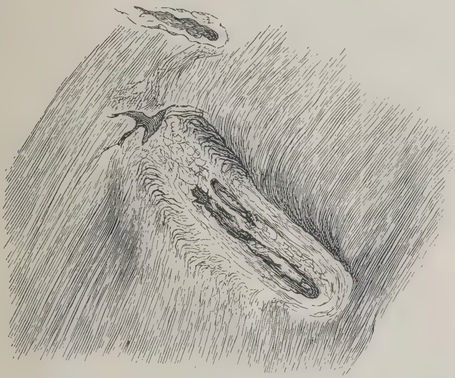

FIG. 73.—Vascular canal in human dentine.

These canals, which occasionally occur both in human and other mammalian teeth, are to be regarded as abnormalities.* There is yet another modification of the vascular canal occurring as an invariable character in certain teeth, which is of great interest from the point of view of evolution, since it exemplifies vascular canals losing their function and in process of disappearance. Towards the

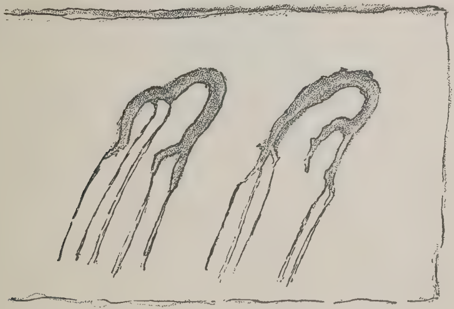

FIG. 74.—Vascular loops from tooth of *Sargus.*

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* This statement may require modification in the light of the above-quoted findings of Mummery in the teeth of *Sarcophilus* and *Cynomys.*—ED.

base of the teeth of *Sargus*, for instance, loops of uniform calibre, with their concavities directed towards the pulp, may be seen. No one familiar with the canals of vaso-dentine can for a moment doubt that they were formed around a vessel, but though such was their origin, the vessels soon ceased to be permeable, and their open ends stop far short of the pulp-chamber, in the midst of the dentine.

It is interesting to note that their ends are not abruptly cut off and sealed, but that they taper down and are continuous with one, two, or three dentinal canals (Fig. 74).

Nothing is known of the contents of these loops in the fresh tooth, but it hardly admits of doubt that this partial persistence of the vascular channel, speedily abandoned in the further building of the dentine, indicates descent from a form in which these canals were functional, and the type of dentine a real vaso-dentine. The walls of these canals are smooth, just as in a typical vaso-dentine, but there is yet another form of canal which, in this respect, has departed a little more from its pristine type.

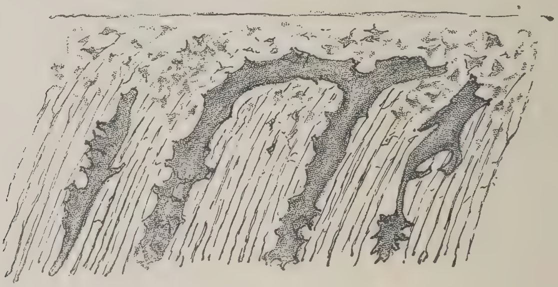

Fig. 75.—Dentine of manatee, showing partial persistence of vascular canals.

In the outer part of the dentine of the manatee a series of regular loops are to be seen (Fig. 75), which at first sight look like, and in the earlier editions of this book were described as, vascular canals. Just as in *Sargus*, their general arrangement and fairly uniform diameter, &c., lead one to the conclusion that they mark the site of former vessels.

But, in place of their interior being smooth, a higher power discloses that it has numerous irregular sharp prolongations running out from it, between which rounded projections encroach upon the lumen of the canal.

In point of fact the walls bounding the canal strikingly recall the walls of an interglobular space, and the whole canal might appropriately be compared to an enormously elongated interglobular space. As in *Sargus*, nothing is known of the contents in the fresh state ; but, as in that fish, it is hardly possible to doubt that here also there is evidence that in some ancestral form there was a circulation through these channels.

The method of their disappearance is interesting; the dentinal tubes run into or past them, and had calcification gone a little further, to the obliteration of the above so-termed "long" interglobular spaces, the last trace of the ancestral vaso-dentine would have disappeared.

Osteo-dentine.—This is a tissue which in its most typical form is marked off from hard dentine, plici-dentine and vaso-dentine alike by certain structural peculiarities and by the method of its development. It sometimes approaches very nearly to bone, from which indeed it has few essential points of difference. But there are many transitional forms, so that it is often hard to draw a sharp line of distinction between them.

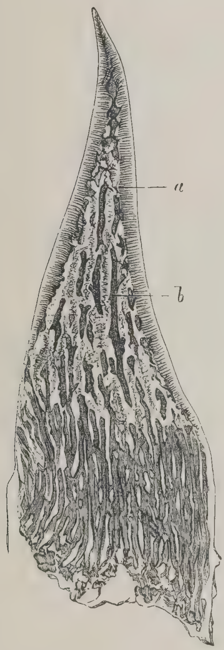

FIG. 76.—Tooth of common pike. *a*. Outer layer of fine-tubed dentine. *b*. Inner mass of osteo-dentine.

The difference can hardly be fully appreciated until the development of dentine has been described; but it may be at once mentioned that osteo-dentine is not wholly formed upon the surface of the pulp, and it results from this that whereas the pulp chamber has a definite outline in those forms thus far described, and the pulp can be bodily pulled out, in osteo-dentine calcified trabeculæ shoot right through the pulp, there is ultimately no sharply defined pulp chamber, and the pulp cannot be pulled out, the hard and soft tissues being inextricably mixed up.

And though there are numerous large channels, often much larger than those of vaso-dentine, they are less regular, do not in their arrangement so closely follow the form of capillary loops and in a fresh tooth contain masses of pulp structure as well as blood-vessels.

The pike's tooth affords a good example of osteo-dentine. Its surface is formed of a layer of fine-tubed tissue, almost like ordinary dentine, but this soon gives place to a coarsely channelled tissue, containing elongated spaces filled with pulp, from which canaliculi, like those of a bone lacuna, branch off in all directions, but do not extend far.

The fine-tubed layer which forms the exterior differs from ordinary dentine in the respect that the tubes, although parallel in their outer portion, in the absence of a general pulp cavity, as they pass inwards become gathered together into fewer and larger tubes, which again originate from the somewhat irregularly shaped channels in the interior of the tooth.

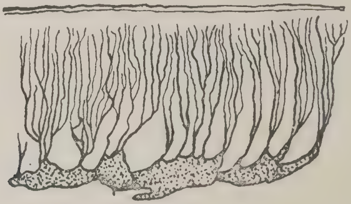

Fig. 77.—Outer layer of the dentine of the tooth of a pike. The fine canals are seen to be gathered into bundles, which spring from the large canals of the axial portion of the tooth. Röse would distinguish this outer layer as normal dentine, postulating a change in the formative cells, which he holds to have been at first odontoblasts, afterwards osteoblasts. But this is an assumption not proven.

Their relationship to the fine tubes which occur in less abundance in the deeper parts of the tooth is thus shown, and the close resemblance of these dentinal tubes to the canaliculi of ordinary bone becomes apparent.

It is stated by Sternfeld (19) that flat cells line all the surfaces, and that processes from these enter the tubes.

The structure of the teeth of sharks shows a large amount of variability; thus the teeth of the great white shark (*Carcharias*), which is so formidable in the tropics, are composed of ordinary fine-tubed dentine, with the exception of their bases, which are of osteo-dentine.

On the other hand, the teeth of the Porbeagle shark (*Lamna*) consist of a central core of osteo-dentine surrounded (?) with enamel (Fig. 78).

In an osteo-dentine, medullary canals of varying size run with a direction, roughly speaking, parallel to the long axis of the tooth, anastomosing with one another, and from their sides wavy bundles of fine tubes radiate, but do not run far ; that is to say, its dentinal tubes do not radiate from any one central pulp chamber, but from an indefinitely large number of canals.

When, as happens in some sharks, these medullary canals are very regular in size, are placed at nearly uniform distances from each other and run parallel with one another towards the surface, a structure not widely different in places from that found in *Myliobates* obtains. But as in *Myliobates* there are few teeth, whereas in most rays there are a great many, it is possible that its structure may be the result of fusion of many denticles, a process actually observed in *Ceratodus*, and in the *Cochliodontidæ*, a family of Palæozoic sharks. Its development is not sufficiently well known to settle the question.*

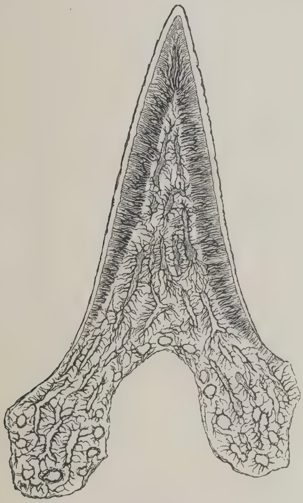

FIG. 78.—Tooth of a species of *Lamna*, consisting of a central mass of osteo-dentine with a fine-tubed tissue, which may probably be regarded as enamel, upon its surface, and which is not homologous with that on the surface of the pike's tooth.

At the other extremity of the series canals much more branched and irregular in their course are found, the tubes radiating from them reduced in amount and extent, some degree of lamination of the matrix, and, in short, a tissue which is practically like ordinary bone.

The similarity of the channels of pulp in osteo-dentine to Haversian canals in bone is in some respects close, so similar that when teeth consisting of osteo-dentine become, as in many fish they do, anchylosed to the subjacent bone, it becomes impossible to say at what point the dentine ends and the bone commences ; and this difficulty is intensified by the fact that the bone of many fishes lacks lacunæ, and is almost exactly like dentine. In many fish the outer compact layer of the jawbone has fine parallel canaliculi, and no other structure is visible, so that it bears a close resemblance to the external layer of these osteo-dentine teeth.

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* Gegenbaur admits the reality of a concrescence in *Ceratodus*, but denies, on the authority of Treuenfels, its occurrence in *Myliobatis*.

Osteo-dentine was defined by Owen as dentine in which the matrix is arranged in concentric rings around the vascular canals, having lacunæ similar to those of bone.

But neither of these characters are to be found in many teeth which, if the manner of their development is to be taken into account, are unquestionably composed of osteo-dentine; and so they cannot be made use of for purposes of definition, although lacunæ and lamination of the matrix are far more often present in osteo-dentine than in the other varieties of dentinal structure.

It will be seen from what has already been stated that the varieties of dentine blend with one another, and it becomes a matter of difficulty to frame satisfactory definitions, especially in the case of osteo-dentine, without taking into account its development.

The varieties of dentine may be grouped thus:

(A.) Dentines developed upon the surface of a pulp, by calcification of its surface layers, dentinal tubes, when present, radiating from a single axial pulp chamber or from its folds.

  (i.) Hard, unvascular dentine, thoroughly permeated with dentinal tubes, which radiate from a simple central pulp chamber. Example—Human dentine.

  (ii.) Plici-dentine, permeated with dentinal tubes, which radiate from a pulp chamber rendered complex in form by infoldings of its walls. Examples—*Lepidosteus*, *Labyrinthodon*.

  (iii.) Vaso-dentine, with dentinal tubes few or absent, but abundant capillary channels with blood circulating through them. Example—Hake.

  (iv.) Dentines which might be regarded as aggregations of fused parallel denticles, as forms of folded dentine, or as transitional towards a very regular osteo-dentine. Examples—*Myliobatis*, *Pristis*.

(B.) Dentines developed by calcification extending through the interior of a pulp, not by calcification of a surface layer. Dentinal tubes have relation to the medullary tracts left, and not to an axial pulp chamber.

  (v.) Osteo-dentine, or trabeculo-dentine, with dentinal tubes which radiate from numerous medullary channels, and which may be only short and few in number, or may be fully developed. Lamination of the matrix and spaces like bone lacunæ occur in some osteo-dentines. Examples—Pike, *Lamna*.

Röse, in a valuable paper (18), points out that, with the exception of true vaso-dentine, which is first known to occur in some cretaceous fish (*Empo-* and *Pachy-rhizodus*), all of the modifications of dentine are found to exist in the earliest known Silurian fish, and he thinks that normal dentine was probably the oldest calcified tissue.

In the same paper Röse proposes a different classification of dentines, viz.:—

Ortho-dentine (under which heading would come Vaso-dentine and Vitro-dentine as subdivisions).
Trabecular dentine.
Osteoid dentine.
Bone dentine.

The criterion which he selects for his definition of normal dentine is that it shall have been developed in an even line from without inwards *immediately under an epithelial sheath*, and therefore will have a single undivided pulp cavity.

I am not in the least concerned to defend my classification because I happen to have proposed it myself, and I have repeatedly pointed out that it is not in all respects satisfactory. But I do not find Röse's classification in practice to be any better, and, in fact, I think that the application of his criterion leads one into difficulties, necessitating the grouping together of forms rather divergent, and separating others, which are practically identical, into different classes. Thus *Carcharias* has distinctly normal dentine, whilst other *Selachia* have, equally distinctly, osteo-dentine. Yet in their relation to the epithelial sheath these two forms are absolutely similar. In like manner the incipient infoldings of such teeth as Varanus (near its base) by Röse's criterion remain normal dentine, but precisely the same sort of folding carried further is called by him trabecular dentine.

To the term trabecular dentine, in itself, I have no objection: indeed, I think it a better descriptive term than osteo-dentine; it is to Röse's application of the term in leading to a grouping together of forms which appear to me essentially different that exception is taken. My reasons for differing from him are given at greater length in a paper (25).

Röse adopts fully my definition of vaso-dentine, but does not retain plici-dentine as a separate distinct variety, although he speaks of "real folds of pure dentine" in *Rhizodus*, *Megalicthys*, &c., my plici-dentines coming under his trabeculo-dentines, where I do not think they belong. And he distinguishes as vitro-dentine some structures which I do not think are distinct or require a distinctive name, *e.g.*, the outer portion of a hake's tooth, which differs in no respect from that which lies deeper, save that the vascular canals stop short of it (cf. p. 98), and brings under this heading others which I consider preferably as enamels, *e.g.*, the hard outer layer of Selachian teeth (cf. p. 62) (C. S. T.).

It remains to be added that the same pulp may undergo a change in the manner of its calcification; that is to say that, after having gone on with surface calcification for a certain length of time, this may give place to a more irregular internal calcification into an osteo-dentine.

This is especially prone to happen after injury, and is often exemplified upon a large scale in elephants' tusks, the pulps of which, normally engaged in calcifying the odontoblast layers into ivory, may after an injury calcify irregularly and solidify into a coarse osteo-dentine.

It will then be easy to understand that so-called secondary dentine, produced in a pulp which ordinarily forms hard dentine, may partake of the character of hard, of vaso-, or of osteo-dentine.

Thus the pulp of a sperm whale's tooth becomes obliterated by a development of secondary dentine, which sometimes forms irregular masses loose in the pulp chamber, and sometimes is adherent to and continuous with the dentine previously formed. The structure of these masses is very confused. Tubes, of about the same diameter as dentinal tubes, abound ; but they are often arranged in tufts or in bundles, and without any apparent reference to any common points of radiation. Irregular spaces, partaking of the character of interglobular spaces or of bone lacunæ, abound ; and vascular canals are also common.

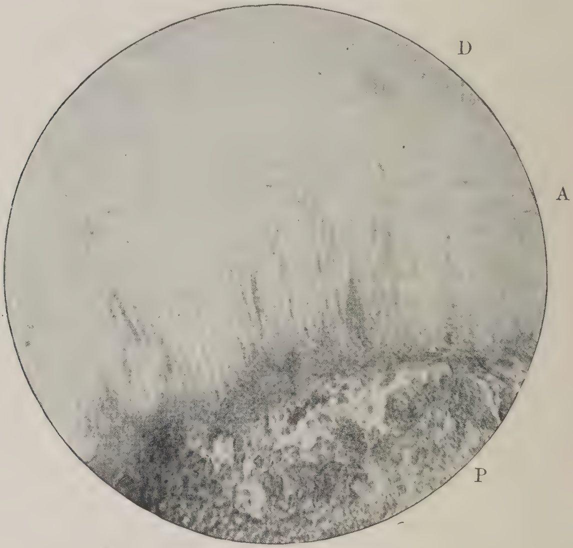

Fig. 79.—Areolar adventitious dentine. × 250. A = areolar dentine; D = primary dentine ; P = pulp tissue. Secondary (adventitious) dentine filling up one of the cornua of the pulp cavity. From a human molar affected by caries.

In the human tooth secondary dentine occurs in the teeth of aged persons, in which the pulp cavity is probably contracted in size, and is also very frequently formed pathologically, as a protection to the pulp when threatened by the approach of dental caries (called by Hopewell-Smith " adventitious dentine ") or by the thinning of the walls of the pulp cavity through excessive wear. The accompanying figure, representing an " erosion cavity " in the neck of a tooth, is a good example of pathological adventitious dentine. It occasionally happens that the pulp resumes its formative activity, and new dentine is developed, which, with the exception of a slight break or bend in the continuity of the tubes, is almost exactly like normal dentine. More often, however, the boundary line between the old and the new is marked by an abundance of irregular spaces and globular contours, whilst further in the mass of new secondary dentine the tubular structure again asserts itself more strongly.

The axial portions of many teeth of persistent growth, for some little distance below the working surfaces, become filled by a calcification which has much in common with the secondary dentines; that is to say, it is of coarser and less definite structure than the peripheral parts of the same tooth.

For example, in the armadillo the axial portion of the tooth is made up of a tubular tissue, but the tubes are crowded together into irregular bundles, and instead of running from the interior towards the surface, they run more or less along the axis of the tooth. In another member of the *Edentata* (the sloth) the axial portion differs much more from the outside, being very much softer and more porous, containing, in fact, a large number of vascular channels, and being very apt to break away in the process of rubbing down the section.

In some rodents the final closure of the axial tract takes place almost by a continuance of the formation of normal fine-tubed dentine with very little secondary dentine of different structure, while in others there is a large area of dentine with vascular tracts in it. In the partly persistently growing incisor of the kangaroo there is a mass of secondary dentine which is sometimes almost glassy-looking and structureless. In some specimens of secondary dentine from an elephant's tusk Howard Mummery found an abundant connective tissue stroma after decalcification.

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CHAPTER IV.

THE TOOTH PULP—CEMENTUM—THE GUM—THE ALVEOLO-DENTAL MEMBRANE.

THE pulp occupying the central chamber or pulp cavity was the formative organ of the dentine, and consequently varies in its anatomical characters according to its age. As well as being the remains of the dentine papilla of the tooth-germ, it is the source of vascular and nervous supply to the dentine.

The pulp may be described as being composed of a very delicate connective tissue with spaces filled with a jelly-like material, the fibres of which are probably principally the processes of the cells. The finely fibrous element of the pulp is not, however, brought into view unless special stains are employed which colour it; if this be done, it is found that there is far less unoccupied space than was formerly supposed. The cells are fairly abundant. Some ordinary fibrous connective tissue is discoverable in it, and nerves and blood-vessels also ramify abundantly in its substance.

The intercellular matrix, remaining in material proportion whilst the cells are not greatly developed and the fibrous element is very delicate, gives to the pulp a character common to many embryonic tissues.

At an early period the cells of the dentine papilla are somewhat rounded embryonic cells, a surface layer of specialised cells, the future odontoblasts, making their appearance only about the time at which calcification commences.

The deeper cells of the pulp are stellate and embryonic in type with well-marked nuclei. They have long anastomosing processes, but these remain very fine, and at no period are large bundles of connective tissue fibres to be found unless the pulp has undergone degeneration in advanced age.

In a specimen cut from a loose tooth in an aged person, which was given to the author by Hopewell-Smith, the cellular, vascular and nervous elements have all completely disappeared, and there remains nothing but connective tissue, the bundles of which run into the dentine. It is possible that the conspicuousness of this connective tissue may partly be due to the fact that it is in no degree concealed by the abundant cells of an ordinary pulp, but it seems probable that the connective tissue itself is also coarser and more abundant.

The entrance of connective tissue fibres into the dentine is of importance in connection with the question of the entrance of nerve fibres into the dentine, and also in relation to the calcification of the dentine. [Hopewell-Smith regards the structures described as nerves as possibly being connective tissue fibres.]

The cellular elements of the pulp are arranged, as seen in transverse sections, in a direction radiating outwards from the centre; this is most marked in the highly specialised layer of cells which form the surface of the pulp, and are termed odontoblasts.

The odontoblast layer, sometimes called the *membrana eboris*, because it usually adheres more strongly to the dentine than to the rest of the pulp, and is therefore often left on the surface of the dentine when the pulp is torn away, consists of a single row of large elongated cells, of a dark granular appearance, with large and conspicuous nuclei near to the ends furthest from the dentine.

The sharp contours possessed by the odontoblasts in pulps which have been acted on by chromic acid, alcohol, or even water, are absent in the perfectly fresh and unaltered condition, and it is believed that they have no special investing membrane. They have two sets of processes, one peripheral and one central. Of these the *dentinal process* (equivalent to the dentinal fibre) enters the canal in the dentine, and the individual odontoblasts may be furnished with several dentinal processes.

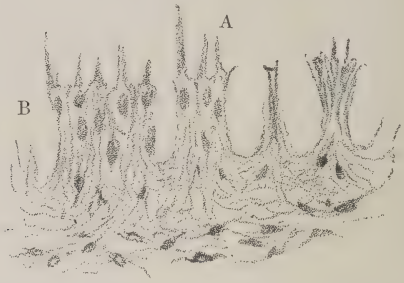

Fig. 80.—Surface of human pulp, showing odontoblasts with their processes. A. Dentinal process. B. Nucleus.

Dr. Aitchison Robertson (12) describes the central or pulp process and the odontoblasts in the ox as being very long and fine, but says that there is no lateral union; his specimens, however, appear to have been mostly teased out, and the cells figured hardly look like odontoblasts.

Lateral processes, by which neighbouring odontoblasts communicate with one another, have been described, but there is some doubt whether they have any real existence. Mummery, however, seems to regard them as definite connecting processes which sometimes become involved in the calcification of the dentine, and which persist as horizontal tubes in the matrix.

When dentine formation has commenced, the odontoblasts are united at their extremities nearest to the dentine by a sort of collar, but this is of the nature of imperfectly formed material, and is not properly a process of the odontoblast cell.

The process which enters the dentinal tubes is of some size, tapers slightly, and extends from the cell in a line coincident with its longitudinal axis. Each cell has one or more such processes, which follow the course of the dentinal tubules described in the preceding chapter. The process is an extension of the cell plasma, and, according to Hamazawa, carries with it a tubular ensheathing extension of the cell membrane.

The *membrana eboris* covers the surface of the pulp like an epithelium. The odontoblasts vary much in form at different periods; in the youngest pulps, prior to the formation of dentine, they are rounded, or rather pyriform. During the period of their greatest functional activity the end directed towards the dentine is more or less square, though tapering to a slight extent into the dentinal process; while in old age they become comparatively inconspicuous and assume a more rounded or ovoid shape. They are altogether larger in the coronal than in the radicular regions of the pulp, and, in transverse sections of the tissue, are seen to be shorter and rounder in its constricted portion than in its longer diameter. In cylindrical pulps their lengths are the same. The odontoblasts are slightly separated from one another, an effect which is rarely seen in the enamel cells—a fact which, if due to shrinkage through the use of histological reagents, would indicate either that they have no definite limiting membranes, or else that they are of a softer material. But it is very possible, especially in view of recent researches into the development of dentine, that they are really slightly separated from one another. They usually, however, adhere together firmly at their ends nearest to the dentine, so as to form here a continuous sheet. The general matrix of the pulp, as has been before noted, is

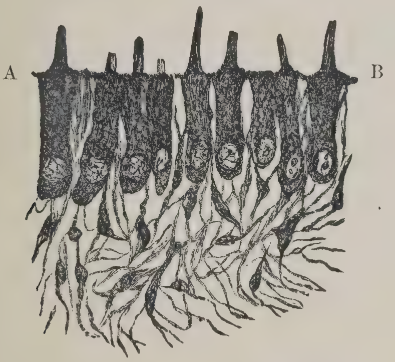

FIG. 81.—Odontoblast cells with their (A) dentinal processes and (B) collars. Beneath and to some extent between them are seen the fusiform cells and connective tissue fibres of the pulp.

of firm, gelatinous consistency; it is a little more dense upon the surface, whence has perhaps arisen the erroneous idea that the pulp is bounded by a definite membrane.

The vessels of the pulp are very numerous; three or more arteries enter at the apical foramen, and, breaking up into branches which are at first parallel with the long axis of the tooth, finally form a capillary plexus immediately beneath the cells of the membrana eboris.

Formerly no lymphatic vessels were known to exist in the tooth pulp. Halle's experiment of injecting Prussian blue into the tissue showed that there are neither lymph spaces nor lymphatic vessels in it. But further experiment by painting Prussian blue upon an exposed pulp in a dog, and sealing it in, proved that somehow the particles passed through the whole pulp and were found in the lymphatic glands, possibly passing by way of the liquid of the tissue, or possibly carried by wandering cells (Morgan,[7]). [More recently, however, Schweitzer and others have demonstrated the existence of lymphatic vessels in the pulp.] The lymphatic glands which receive the products from the teeth and gums are, according to Morgan:

(i.) The supra-hyoid glands, which lie between the bellies of the digastric muscle, drain the anterior part of the lower gums and teeth, and pass the lymph on to the submaxillary group, which are numerous and small. These lie in the digastric triangle along the lower edge of the jaw.

(ii.) The superficial cervical glands which lie along the course of the external jugular vein receive some lymph from the posterior part of the gum, while the deep cervical lie along the internal jugular; indirectly through the submaxillary group they receive lymph from the structures of the mouth.

According to the text-books the lymph from the upper gums and teeth is received by the deep facial glands; they are situated by the side of the pharynx behind the buccinator muscles, and it is suggested by Morgan that cases of suppuration in these glands may not be recognised, but be mistaken for quinsy, as they are close to and behind the tonsil. But for some unknown reason suppuration in the lower lymphatic glands is far more common than in these upper ones.

The nerves enter the apical foramen of the root by one large trunk and three or four minute ones. After pursuing a parallel course, and running in close association with the vessels, meanwhile giving off some branches which anastomose but little in the expanded portion of the pulp, they lose their medullary sheaths, and breaking up into brush-like tufts, form a rich plexus beneath the membrana eboris, as has been described by Raschkow and many subsequent writers. Mummery is of opinion that the large nerve trunks are accompanied by fine branches from the sympathetic system, and which may have trophic functions.

But here our exact knowledge almost ends, for the nature of the terminations of the nerve fibres in the pulp is not with certainty known; the nerve fibrils, which are extraordinarily abundant near to the surface of the pulp, often form meshes, but this does not appear to be their real termination.

Boll, as has already been mentioned, investigated this point, and found that if a pulp be treated for an hour with very dilute chromic acid solution, an immense number of fine non-medullated nerve fibres, which he succeeded in tracing into continuity with the larger medullated fibres, may be discerned near to the surface of the pulp. The ultimate destination of these nerve fibres is uncertain; but he has seen them passing through the membrana eboris, and taking a direction parallel to that of the dentinal fibrils in such numbers that he infers that they have been pulled out from the canals of the dentine. Still, whatever may be the probabilities of the case, he has not seen a nerve fibre definitely pass into a dentinal canal, and the observations of Morgenstern (8), Römer (14) and others are not convincing, as Golgi's staining method may lead to false appearances.

Howard Mummery, using as a stain an iron salt followed by tannin, has succeeded in showing that from the nerve bundles which are distributed to the surface of the pulp very fine fibres are given off, which run towards the dentine, and the author has examined these preparations with him. Whilst there are appearances suggestive of their entering it, no certain conclusion could be reached, such is the difficulty of an investigation where very delicate structures are in relation with a calcified material. Nevertheless, recently, by staining according to the method of Ramon y Cajal, Mummery is of the opinion that nerve fibres do actually penetrate the dentinal tubes. As has been stated in the previous chapter, Mummery's observations seem to have been confirmed by Deppendorf (p. 87).

[From further observations of a more recent date, Mummery has described (10) a definite arrangement of "end-cells" amongst the odontoblasts, the axons of which enter the dentinal tubules accompanying the dentinal fibrils. The dendrons of the end-cells ramify around the odontoblasts, forming synaptic connections both with the dendrons of other end-cells and with nerve fibrils in the plexus of Raschkow.]

Retzius (12) investigated the nerves of the teeth in some fish, batrachians and reptiles, using Golgi's stain and finding practically similar conditions in all. Fine non-medullated fibres pass upwards in the pulp, subdividing as they go. They are beaded, and arrive at the region of the odontoblasts where they end close to the dentine, but they were never observed to enter it. Their actual terminations were fine short ramifications, and now and then the ends are swollen into little knobs, the apices of the pulps being without nerves. In fish, the nerves break up into a plexus in the soft tissues between the teeth, and only fine non-medullated fibres enter the pulps at all. In young mice the ultimate fibrils, beaded as in fish and reptiles, pass between the odontoblasts and there terminate in free ends, and do not penetrate into the dentine.

Carl Huber (4) employed methylene blue, injected into the carotids of rabbits and cats immediately after death. He states that nerves course up the pulp in bundles of eight or ten medullated fibres, which towards the surface anastomose by exchange of fibres or by actual branching at the nodes of Ranvier. Below the odontoblast layer they break up into numerous beaded non-medullated fibres and form a plexus by crossing and recrossing. They terminate by fine ends or granules near to the free ends of the odontoblasts, sometimes appearing almost to enclose the cells in a basket-work of fibres. He states that they never make any connection with the odontoblasts nor could they be expected to, being themselves epiblastic and the odontoblasts mesoblastic in origin.* A few medullated fibres reach as far as the odontoblasts. These observations are therefore in complete accord with those of Retzius, and have been, to some extent, confirmed by Hopewell-Smith (^{3b}).

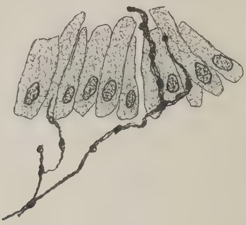

FIG. 82.—Non-medullated nerves ending amongst the odontoblasts. (After C. Huber.)

Boll's observations have not been fully confirmed by any subsequent worker in the field, nor had they been definitely controverted until Legros and Magitot (5) stated that they had fully satisfied themselves that the nerves become continuous with the branched somewhat stellate cells which form a layer beneath the odontoblasts, and through the medium of these cells with the odontoblasts themselves. (See Fig. 55.)

If this view of their relation to the nerves were correct the sensitiveness of the dentine would be fully accounted for without the necessity for the supposition that actual nerve fibres enter it, for the dentinal fibrils would be in a measure themselves prolongations of the nerves.

Dr. Robertson (*loc. cit.*) describes the nerves of the tooth pulp of the ox, his specimens mostly having been made by teasing fresh pulp in 1 per cent. solution of osmic acid. He describes large bundles of medullated and non-medullated fibres, the former being the more numerous, and in the teased specimen the axis-cylinder of medullated fibres was often seen stretching far beyond the sheath. He believes that the axis-cylinders of medullated nerves lose their sheath, and after running for a greater or less distance, become continuous with the pulp process of the odontoblasts, which therefore, with their dentinal processes, become nerve-end organs, so that he so far agrees with Magitot.

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* See footnote on p. 85.

Oscar Römer (14), using the intra-vitam method of methylene blue staining, agrees with Retzius and Huber up to a certain point, but further states that the fine fibres, after passing between the odontoblasts, actually enter the dentinal fibrils and so pass into the dentine, but his figures fail to exclude the presumption of error. Morgenstern (8) goes yet further and says that two axons enter each canal and reach the outer boundary of the dentine, or even pass into the enamel.

It will hence be seen that some uncertainty still attaches to the odontoblasts and their functions, but to this it will be necessary to recur in treating of the development of the dentine.

This difference of opinion as to the function of the odontoblast cells never can be finally settled until the nerve endings of the pulp are satisfactorily demonstrated. The idea that the odontoblasts themselves are nerve-end organs was advocated by Coleman, and more recently in a modified form by Hopewell-Smith (3); but there are some objections to this view, amongst others being the occurrence of well-marked odontoblasts in places where they seem not only useless but decidedly misplaced as nerve-end organs, and the observation of Retzius that there are parts of teeth where there are odontoblasts, but which are not reached by any nerve fibres at all.

Towards the outer surface of the pulp, but beneath the odontoblasts, Weil has described a layer about which there has been, and indeed still is, some controversy. It goes by the name of the "basal layer of Weil," and consists of a comparatively pale and transparent zone lying between the inner ends of the odontoblasts and the pulp. He describes it as consisting of fine connective tissue fibres which communicate with the processes of the odontoblasts. Howard Mummery (9) points out that though visible in many of his preparations made by the Koch-Weil process, it is absent near to the growing base of young teeth, and it is in the crown that it is most pronounced. He disagrees with Weil as to the connection of the fibres of this layer with the odontoblasts, saying that he has often traced these fibres through the cell layer into the dentine matrix. Von Ebner altogether doubts its existence, attributing it to the pulp shrinking while the odontoblasts are held up to the dentine by their processes. Röse shares von Ebner's view. Weil compares it to a basement membrane, urging that a fibrillar structure has been detected in many undoubted basement membranes, but whether it be an actual or an artefact structure, there seems little reason to regard it as anything more than connective tissue pulp stroma.

Walkhoff regards it as a result of atrophy of the odontoblast layer, and says it does not exist in young active pulps. But this is not in conformity with recent research.

It has already been mentioned that the pulp undergoes fibroid alterations in advanced age, its diminution in size, at times, by its progressive calcification and the addition thus made to the walls of the pulp cavity being the most conspicuous changes which occur. In pulps which have undergone a little further degeneration, the odontoblast layer becomes atrophied, and the fibrillar connective tissue more abundant, coincidently with the diminution in the quantity of the cellular elements. Finally, the capillary system becomes obliterated by the occurrence of thrombosis in the larger vessels, the nerves undergo fatty degeneration, and the pulp becomes reduced to a shrivelled, unvascular, insensitive mass. These changes may go on without leading to actual putrefactive decomposition of the pulp, and are hence not attended by alveolar abscess ; but a tooth in which the pulp has undergone senile atrophy is seldom securely attached to its socket.

The pulps of the teeth of some animals become eventually entirely converted into secondary dentine, but it would seem to be very generally the case that those teeth which exercise very active functions and last throughout the life of the creature retain their pulps in a more or less active condition.

CEMENTUM.

This tissue forms a coating of variable thickness over the roots of the teeth, sometimes, when the several roots are very close to one another, or the cementum is thickened by disease, uniting the several roots into one.

The cementum is ordinarily said to be absent from the crown of the teeth of man, the carnivora, &c., and to commence by a thin edge just at the neck of the tooth. As mentioned in a preceding chapter, the cement may either overlap slightly the enamel, or be overlapped by it. Occasionally the two tissues do not meet, thus leaving the dentine at the neck of the tooth exposed. The cementum is, in normal circumstances, thickest in the interspaces between the roots of molar or premolar teeth ; it is, however, often thickened at the end of a root by a pathological hyperplasia. In compound teeth, the cementum forms the connecting substance between the denticles (see the figures of the tooth of the *Capybara*, the elephant, &c.), and, before the tooth has been subject to wear, forms a complete investment over the top of the crown. The cementum also covers the surfaces of the complex-patterned crowns of the teeth of ruminants. Here it is the most external of the dental tissues, a fact which necessarily follows from its being derived more or less directly from the tooth follicle.

Both physically, chemically, and also in respect of the manner of its development, the cementum is closely allied to bone. It consists of a laminated calcified matrix or basal substance, and, if large in amount, lacunæ. Vascular canals corresponding to the Haversian canals of bone may be rarely met with, but it is only in thick cementum that they exist and, in man, perhaps in hyperplasia more often than in the thick healthy tissue.

The lamellæ of the cementum are thinner towards the neck of the tooth, being thickest at the apex of the root, but the number of the lamellæ is about the same in all parts. [They are more apparent in ground sections, and are separated by light lines, which, since they suggest intermittent formation of the tissue, have been termed by Salter "incremental lines."]

Soon after the completion of a tooth, there are but few lamellæ, so that usually an adult has cementum far thicker than a child, an aged person again perhaps having more than an adult.

The matrix is a calcified substance, which, when boiled, yields gelatine, and if decalcified, retains its form and structure ; it is, in fact, practically identical with the matrix of bone. It is sometimes apparently structureless, at others finely granular, or interspersed with small globules.

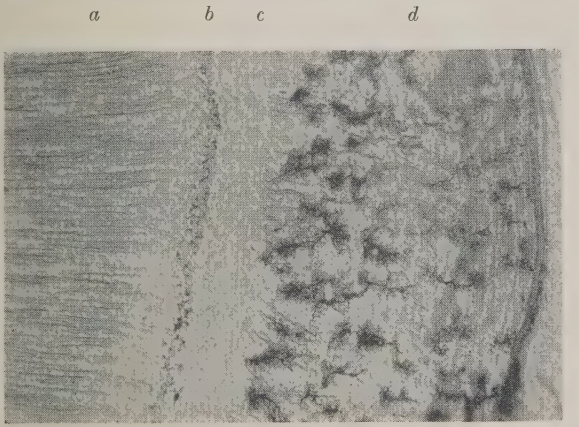

Fig. 83.—Thick laminated cementum from the root of a human tooth. *a*. Dentine. *b*. Granular layer of Tomes. *c*. Normal cementum. *d*. Hyperplasic cementum. Ground section, unstained. (C. B. H.)

The lacunæ of hyperplasic cementum share with those of bone the following characters : in dried sections they are irregular cavities, elongated in the direction of the lamellæ of the matrix, and furnished with a large number of processes. The processes of the lacunæ (known as canaliculi) are most abundantly given off at right angles to the lamellæ (see Fig. 83), and, again, are more abundantly directed towards the exterior of the root than towards the dentine. The lacunæ differ from those of bone in being far more variable in size, in form, and in the excessive number and length of their canaliculi. In this latter respect the lacunæ of the cementum of cetacean teeth are very remarkable.

Many of the lacunæ are connected, by means of their canaliculi, with the terminations of the dentinal tubes (Fig. 84) ; they, by the same means, possibly intercommunicate with one another, while others of their processes are directed towards the surface, which, however, in most instances, they do not appear actually to reach.

The lacunæ assume all sorts of peculiar forms, especially in the thicker portion of the cement.

Here and there lacunæ are to be found which are furnished with comparatively short processes and are contained within well-confined contours. Sometimes such a line is to be seen surrounding a single lacuna, sometimes several lacunæ are enclosed within it; lacunæ so circumscribed are called "encapsuled lacunæ," and were first observed by Gerber in the cementum of the teeth of the horse (they are specially abundant in the teeth of the *Perissodactyla*). By cautious disintegration of the cementum in acids these encapsuled lacunæ may be isolated, their immediate walls, just as in bone, being composed of a material which has more power of resisting chemical reagents than the rest of the matrix.

The encapsuled lacunæ may perhaps be regarded as individual osteoblasts, or nests of osteoblasts, which have to some extent preserved their individuality during calcification.

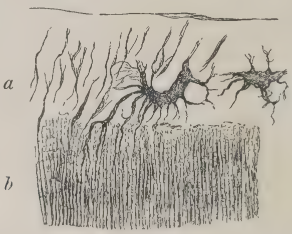

Fig. 84.—Lacuna of cementum which communicates with the terminations of the dentinal tubes. *a*. Cementum. *b*. Dentine.

In the fresh condition it appears probable that the lacunæ are filled up by soft matrix, which shrinks, and so leaves them as cavities in dried sections. It can hardly as yet be said that the question of the contents of the lacunæ has been finally settled, though the researches of Bödecker and Heitzmann have gone far towards doing so.

According to these and other writers each lacuna contains a protoplasmic body, which they term the cement corpuscle, with a central nucleus. This nucleus may be large and surrounded by but little protoplasm, or it may be small; or there may be many nuclei.

Heitzmann, after staining with gold chloride, claims to have demonstrated protoplasmic matter in the thin layer of cementum of the neck of the tooth, and while the author by no means agrees with him in regarding as protoplasm everything which will stain with chloride of gold, yet clinically there would seem to be very little doubt that the cementum in this locality is sensitive, and that there is an *a priori* probability that there is some uncalcified tissue there. At the same time it must be remembered that semi-calcified tissue can be stained with silver nitrate, and sometimes also with gold, on the periphery of the pulp, in interglobular spaces, and in Neumann's sheaths, and one would quite expect to find, in the interstices of such globular forms as can be made out in this thin cementum layer, such semi-calcified matrix material.

Heitzmann also throws doubt upon the perforating fibres that are to be described as being Sharpey's fibres ; he interprets them also as protoplasmic, in which view few histologists will share.

The cementum corpuscles communicate freely with one another by offshoots, those of large size occupying the conspicuously visible canaliculi of the lacunæ, whilst the finer offshoots are believed by Heitzmann to form a delicate network through the whole basis substance or matrix. The corpuscles of the cementum near to the external surface give off numerous offshoots which communicate with protoplasmic bodies in the alveolo-dental periosteum. By this means it would appear as if the cementum can remain alive even when the pulp of the tooth is dead, and thus the tooth be in no way a mere foreign body, dead and inert.

[Hopewell-Smith distinguishes between " perforating fibres " and " Sharpey's fibres." The former term he applies to structures crossing the cemento-dentinal junction, and which, according to Black, are the calcified remains of the principal fibres of the peri-odontal membrane.]

Like bone, cementum contains Sharpey's fibres ; that is to say, minute rods running through it at right angles to its own lamination, and, as it were, perforating it. These are probably calcified or uncalcified bundles of connective tissue. And it is by the medium of these that the alveolo-dental periosteum adheres to the cementum.

Where the cementum is very thin, as, for instance, at the neck of a human tooth, it is generally to all appearances structureless, and does not contain any lacunæ and therefore no protoplasmic bodies ; nevertheless, lacunæ may be sometimes found in thin cementum, as, for example, in that thin layer which invests the front of the enamel of the rodent-like tooth of a wombat.

Hopewell-Smith is of the opinion, based on the examination of many sections, that there are no lacunæ in perfectly healthy human cementum, and that their presence is a sign of subsequent pathological increase in the tissue. He believes that cementum *per se* is insensitive, but that tactile sensations may be conveyed through it to the underlying dentine.

The cementum at the neck is also devoid of lamellæ ; it appears to be built up by direct ossification of osteoblasts, the characteristic shape of which may be traced in it. Bödecker describes it as permeated by a fine but abundant network of soft living matter. The larger dentinal tubes fall short of the boundary line at the neck, but according to him a fine protoplasmic network crosses it. He states that it has a covering of epithelial elements, like those of the gum.

The outermost layer of thick cementum is a glassy film, denser apparently than the subjacent portions, and quite devoid of lacunæ, being homologous with the peripheric lamellæ of the long bones. On the surface it is slightly nodular, and may be described as built up of an infinite number of very minute and perfectly fused globules ; this is, in fact, the youngest layer of cement, and is closely similar to that globular formation which characterises dentine at an early stage of its development.

The cementum is very closely, indeed inseparably, connected with the dentine, through the medium of the "granular" layer of the latter, the fusion of the two tissues being so intimate that it is often difficult to say precisely at what point the one may be said to have merged into the other. [Between the granular layer and the cementum a layer of homogeneous material can very frequently be distinguished, which Hopewell-Smith regards as a layer of structureless dentine. This layer appears to be marked off from the cement by a dark line.] And in this region there is an abundant passage of protoplasmic filaments across from the one to the other.

Nasmyth's Membrane.—Under the names of "Nasmyth's membrane," "enamel cuticle," or "persistent dental capsule," a structure is described about which much difference of opinion has been, and indeed still is, expressed. Over the enamel of the crown of a human or other mammalian tooth, the crown of which is not coated by a thick layer of cementum, there is an exceedingly thin membrane, the existence of which can only be demonstrated by the use of acids, which cause it to become detached from the surface of the enamel. When thus isolated it is found to form a continuous transparent sheet, upon which, it is said, by staining with nitrate of silver, a reticulated pattern may be brought out, as though it were made up of epithelial cells. It is exceedingly thin, Kölliker attributing to it a thickness of only one twenty-thousandth of an inch, though probably this is incorrect ; nevertheless, it is very indestructible, resisting the action of strong nitric or hydrochloric acid, and only swelling slightly when boiled in caustic potash. Notwithstanding, however, that it resists the action of acids, it is not so hard as the enamel, and becomes worn off tolerably speedily, so that to see it well an unerupted tooth, still enclosed in its dental capsule, should be selected.

The singular power of resistance to reagents which characterises it proves nothing more than that it is a tissue, imperfectly calcified, on the border-land of calcification, so to speak, since similarly resistant structures are to be found lining the Haversian canals, the dentinal tubes, the surface of developing enamel, the lacunæ, &c. When burnt it gives off a smell like that of burning horn.

In Sir John Tomes' opinion (17) it was to be regarded as a thin covering of cementum, and the author gave additional evidence in support of this view in a paper referred to hereafter.

More recent investigations of Paul (11) have, however, thrown a fresh light upon the matter, and have shown that the points upon which the author chiefly relied are open to quite a different explanation. He employed unworn teeth, fixed in a chromate solution, and detached the membrane by a 5 per cent. solution of nitric acid; he has since simplified the process by decalcifying the enamel at once by immersion in a phloroglucin and nitric acid solution without preliminary fixation. The membrane can easily be stained in eosin or in Ehrlich's acid hæmatoxylin, washed, and mounted in Farrant's medium.

This at once shows the reticulated pattern; but that this is not due to the impressions of the ends of the enamel prisms is proved by its being too large—ten times too large according to Paul—and, in addition, there are large nuclei which are so related to the pattern as to show that it is produced by the margins of the cells of which they are the nuclei. His specimens, from one of which Fig. 85 is taken, leave no doubt but that it is a membrane composed of a layer of flat epithelial cells.

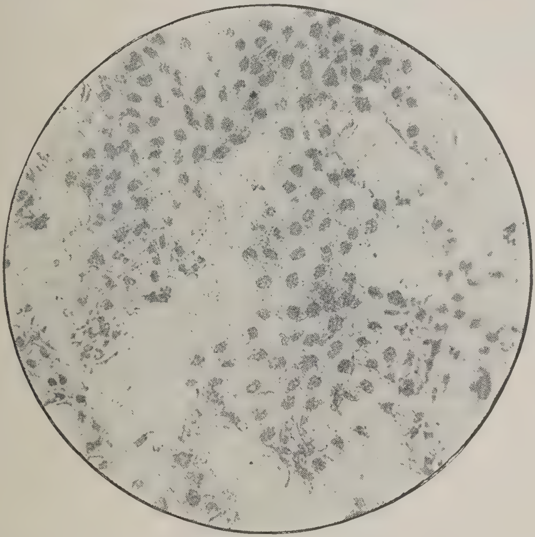

FIG. 85.—Nasmyth's membrane, showing the stained nuclei. From a specimen prepared and photographed by Dr. Paul.

It is obvious that a layer of flat epithelial cells in this situation can have only one source, namely, some part of the enamel organ, and Paul found that in cutting sections of the dental capsule he was able to find upon its inner surface a layer of flat epithelial cells, which could be traced to be the external epithelium of the enamel-organ. Hence the present state of knowledge on the subject must lead to the conclusion that Waldeyer was right, and that Nasmyth's membrane is a product of the external layer of the enamel-organ.

In addition to the layer of epithelial cells, there is a thin structureless pellicle inside them, *i.e.*, between them and the enamel, which is of such consistence as to make the isolated Nasmyth's membrane tend to curl up. Upon the inner surface of this membrane the pitted impressions of the ends of the enamel prisms may sometimes be seen, as described by the older observers.

Like the epithelial layer, this membrane must, from its position, be a product of the enamel-organ. Paul suggests that it may be of some service in protecting the enamel by its power of resistance to acid, especially in those depressions which are the most vulnerable points in a tooth, from which it would not get worn off as it does from the more exposed regions. It seems possible that this inner portion may be merely a sheet of imperfectly calcified enamel, the last products of the effete enamel cells, and so correspond with the thin sheet of tissue which may be raised from the surface of forming enamel at all stages of its growth.

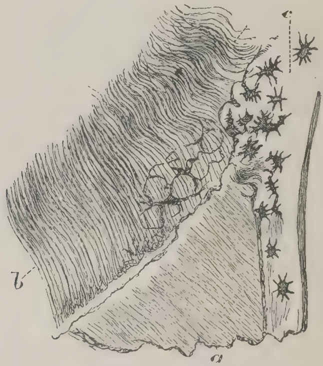

Fig. 86.—From a section of a premolar tooth, in which the cementum, *c*, is continued over the outside of the enamel, *a*. The dentine is indicated by the letter *b*.

Several views have been held as to the nature of Nasmyth's membrane. It has been thought (1) to be a thin layer of cementum, too thin to show the characteristic structure of cementum, as supposed by Sir John Tomes and by the author; (2) to be a final product of the enamel cells or ameloblasts (Kölliker); (3) to be derived from the external epithelium of the enamel organ.

The grounds upon which the author believed it to be a thin layer of cementum were that in a large number of animals there is a thick and functional layer of cementum outside the enamel, and that it now and then happens that the cementum upon a more or less abnormal human tooth, instead of terminating at the neck of the tooth, is continued up over the exterior of the enamel. This occurs less uncommonly than is generally imagined, and the foregoing Fig. 86 represents a portion of the crown of such a tooth.

If sections be made of the grinding surfaces of such teeth as present rather deep fissures in these situations, well-marked and unmistakable lacunal cells, or encapsuled lacunæ, will be met with occasionally. Now and then an encapsuled lacuna may be found occupying a shallow depression in the enamel which it just fits, but more commonly a dozen or more are crowded together in a pit in the enamel, where they are usually stained of a brownish colour. The occurrence of lacunæ in these situations is far from rare; Sir John Tomes' collection contains several good examples of them in these positions.

Nasmyth's membrane, thin though it is over the exterior of the enamel, is thickened when it covers over a pit or fissure, and when isolated by an acid is seen to have entirely filled up such spots (Fig. 88).

In these places, then, where the encapsuled lacunæ are to be found, Nasmyth's membrane also exists, a fact which alone would lend some probability to the view that it is cementum.

The general absence of lacunæ in Nasmyth's membrane might be due to the fact that it is not thick enough to contain them, just as the thinnest layers of unquestionable cementum also are without lacunæ.

In sections of an unworn premolar which was treated with acid subsequently to its having been ground thin and placed upon the slide, the author has several times been fortunate enough to get a view of the membrane *in situ*; it then appears to be continuous with an external layer of cementum, which becomes a little discoloured by the acid employed to detach Nasmyth's membrane from the enamel. Caush apparently had observed the same thing when he wrote (²), that Nasmyth's membrane seems to be continuous not with the cementum but with the membrane covering the cementum, that it will stain with fuchsin, and that there is no apparent difference between that covering cementum and that covering enamel.

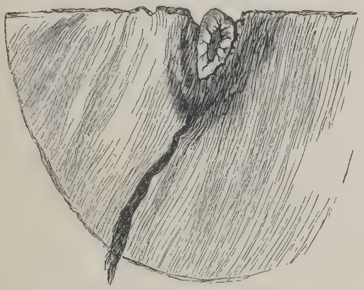

FIG. 87.—Encapsuled lacuna occupying a pit in the enamel.

It is pointed out by Underwood that these observations are not wholly discordant with those of Paul, inasmuch as by the time Nasmyth's membrane is formed the cells of the external epithelium of the enamel-organ are fused with the dental capsule from which cementum is developed. The author was formerly inclined to regard it as young and incomplete cementum, and to consider it as representing (upon the human tooth) the thick cementum which covers the crowns of the teeth of Herbivora; and Magitot, who made many researches upon this subject, entirely concurred in this view, which had also the support of Professor Wedl.

It has, however, been pointed out by Paul that these observations are not inconsistent with the interpretation of its nature which he advocates, for the dental capsule envelops the crown of the tooth in man as well as in certain herbivorous animals, in which it does form coronal cementum; and it is quite possible that it might deposit encapsuled lacunæ in pits where there was room for them, and that these would appear to be in Nasmyth's membrane, which also extends into the pits; nor is its apparent continuity with the cementum at the neck more difficult to account for. To render the matter certain, Nasmyth's membrane should be demonstrated between the enamel and cementum in the teeth of animals possessing thick coronal cementum, but on this point Paul is not, as yet, prepared to speak with certainty.

Nasmyth, who first called attention to its existence, regarded it as the "persistent dental capsule," a view of its nature not very materially differing from that formerly advocated in these pages.

Professor Huxley described it as being identical with the *membrana performativa*; that is to say, with a membrane which covered the dentine papilla prior to the occurrence of calcification, and which afterwards came to intervene between the formed enamel and the enamel-organ. The objections to the acceptance of this view of its nature are so inextricably wrapped up with other objections to Professor Huxley's theory of the development of the teeth that they cannot profitably be detailed in this volume; it will suffice to say that evidence and the weight of authority alike point to there being no such true membrane as this *membrana performativa* in the place in question.

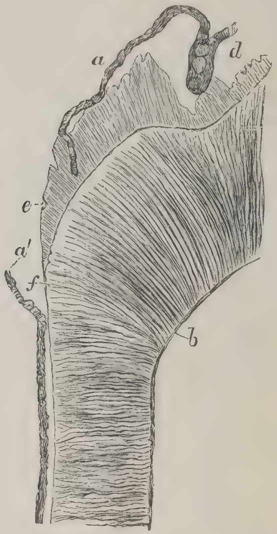

Fig. 88.—Nasmyth's membrane, set free by the partial solution of the enamel. *a*. Nasmyth's membrane. *b*. Dentine. *d*. Mass occupying a pit in the enamel. *e*. Enamel. *a′*. Torn end of Nasmyth's membrane. *f*. Termination of the cementum.

Waldeyer and Röse hold that it (*i.e.*, Nasmyth's membrane) is a product of a part of the enamel-organ. After the completion of the formation of the enamel they believe that the cells of the external epithelium of the enamel-organ become applied to the surface of the enamel and there *cornified*; in this way they account for its resistance to reagents, and for its peculiar smell when it is burnt.

According to the statement of Legros and Magitot, the layer of cells in question (external epithelium of the enamel-organ) is atrophied before the time of the completion of the enamel—a fact which, if confirmed, is fatal to Waldeyer's and Paul's explanation. This is a point which requires to be investigated afresh in the light of recent researches. Magitot, in a later paper (5) on the subject, gives his adherence to the view that it is cementum.

Kölliker, who dissents strongly from the views of Waldeyer, and admits some uncertainty as to its nature, provisionally regards it as a continuous and structureless layer furnished by the enamel cells after their work is completed.

[Mummery (10) after showing that the cellular layer is not one cell thick, but is in many places increased to several layers, calls attention to the presence in many cells of amitotic division of the nucleus without division of the cell-body, and records the opinions of Dahlgren and Kepner, Wilson, and von Rath, that this condition is found in a degenerating cell towards the end of its life.

He calls attention also to rounded cell-masses and definite cell-nests, which apparently represent a late stage in degeneration and keratinisation, and to elongated cells suggestive of altered and shrivelled ameloblasts.

From an examination of longitudinal sections of the tooth in the follicle he has formed the opinion that the membrane consists of cornified cells of the whole enamel-organ (excepting the stellate reticulum), and that attached to its external surface are other altered and degenerated cells which compose the rounded cell-masses and cell-nests.

He appears to agree with Leon Williams that the pellicle is the persisting internal ameloblastic membrane.]

THE GUM.

The gum is continuous with the mucous membrane of the inside of the lips, of the floor of the mouth, and of the palate, and differs from it principally by its greater density. Its tenacity is in part due to the abundant tendinous fasciculi which it contains, and in part to its being closely bound down to the bone by the blending of the dense fibrous fasciculi of the periosteum with its own. The fasciculi springing from the periosteum spread out in fan-like shape as they approach the epithelial surface. There is thus no sharp line of demarcation between the gum and the periosteum when these are seen in section *in situ*.

The gum is beset with rather large, broad-based papillæ, which are sometimes single, sometimes compound. The epithelium is composed of the *stratum corneum*, the *stratum lucidum*, and the *stratum granulosum* ; and cylindrical cells, the *rete Malpighi*, form its deepest layer.

Small round aggregations of pavement epithelium are met with at a little depth, or even imbedded in the surface. In or in the neighbourhood of developing tooth-sacs epithelial aggregations, the so-called "glands of Serres," may be seen, and are remains of the dental-lamina, or tooth-band, which has undergone fenestration subsequently to the completion of its original function. The gums are rich in vessels, but remarkably scantily supplied with nerves. Mucous racemose glands abound.

Black considers that the "glands of Serres" are not glands, but he believes that their constituent cells resemble connective tissue cells, and hence does not apparently think that they are epithelial "nests."

At the necks of the teeth the gum becomes continuous with the periosteum of the internal surface of the alveoli, into which it passes without any line of demarcation.

THE ALVEOLO-DENTAL MEMBRANE.

The Alveolo-dental Periosteum, or Periodontal Membrane, is a connective tissue of moderate density, devoid of elastic fibres, and richly supplied with nerves and vessels.

It is thicker near to the neck of the tooth, where it passes by imperceptible gradations into the gum and periosteum of the alveolar process, than in other parts. The general direction of the fibres is transverse; that is to say, they run across from the alveolus to the cementum, without break of continuity, as do also many capillary vessels. A mere inspection of the connective tissue bundles, as seen in a transverse section of a decalcified tooth in its socket, will suffice to demonstrate that there is but a single "membrane," and that no such thing as a membrane proper to the root and another proper to the alveolus can be distinguished; and the study of its development alike proves that the soft tissue investing the root, and that lining the socket, are one and the same thing: that there is but one "membrane," namely, the alveolo-dental periosteum.

At that part which is nearest to the bone the fibres are grouped together into conspicuous bundles; it is, in fact, much like any ordinary fibrous periosteum. On its inner aspect, where it becomes continuous with the cementum, it consists of a fine network of interlacing bands, many of which lose themselves in the surface of the cementum.

But although there is a marked difference in histological character between the extreme parts of the membrane, yet the markedly fibrous elements of the outer blend and pass insensibly into the bands of the fine network of the inner part, and there is no break of continuity whatever.

The actual attachment, both to the cementum and to the bone, takes place by means of the connective tissue fibres, which pass right into the hard structures, which they traverse for some distance, and in this situation are known as Sharpey's fibres.

They pass through all the lamellæ of the cementum, and there are appearances of shrinkage in dry preparations which would lead to the inference that they were not very fully calcified; in some portions of the cementum it seems to be almost composed of them, as at the neck of a tooth (Black). This writer states that they may be especially clearly seen in the pig, and that "they are the principal fibres of the peridental membrane included in the cementum in its growth, and furnish the means of taking firm hold of the peridental membrane upon the root of the tooth. They are white connective tissue fibres, the ends of which are included in the matrix of the cementum sufficiently to make them apparent when the calcium salts are removed, but when both are calcified they cannot be demonstrated except in cases where there is imperfect calcification of the fibres, as has been mentioned above."

The thickness of the membrane appears to undergo a diminution with age, by calcification encroaching upon it from both the side of the bone and of the cementum.

Malassez (6) urges that an ordinary periosteum in this situation would be too tender for the purposes of mastication and that as it is not a mere enveloping membrane, but is composed of fibrous bundles, which serve to "sling the tooth in its place," it should be called the alveolo-dental ligament. He further compares it with the fibrous bands which in some fishes serve to tie the tooth down to the bone where no tooth sockets exist, and holds that it is strictly homologous with these.

At the surface of the cementum it is more richly cellular, and here occur abundantly large soft nucleated plasma masses, which are the osteoblasts concerned in making cementum.

The fibres, whether in longitudinal or in transverse sections, rarely pass straight in the shortest possible line from the bone to the cementum, but they usually pursue an oblique course, which probably serves to allow for slight mobility of the tooth without the fibres being stretched or torn.

Black (1) gives the following account of the direction of the fibres : Near the neck of the tooth some of the fibres arch over the summit of the alveolus and blend with the periosteum under the gum. A little lower down they pass across horizontally, though when seen in transverse sections they do not pass quite directly, but are more or less tangential to the surface of the cementum, while in the apical half of the tooth they have an upward direction as they pass from the cementum to the bone.

The blood vessels are most abundant in the membrane midway between the bone and the cementum, or rather nearer to the latter, but close to it there is a rich capillary plexus without large vessels. A good many of the arteries enter the apical region and divide to be distributed partly to the tooth pulp and partly to the periosteum, some of them passing from the apex to the gum ; they anastomose freely with vessels in the bone and with those of the gum, so that the blood supply is not easily interfered with.

The vascular supply of the root membrane is, according to Wedl, derived from three sources : the gums, the vessels of the bone, and the vessels destined for the pulp of the tooth, the last being the most important.

The nerve supply also is largely derived from the medullated nerves distributed to the dental pulps ; other filaments come from the inter-alveolar canals, viz., those spaces in the bone, containing nerves and vessels, which are situated in the septa separating the alveoli of contiguous teeth.

It should be borne in mind that the tooth pulp and the tissue which becomes the root membrane have sprung from the same source, and were once continuous over the whole base of the pulp. A recognition of this fact makes it easier to realise how it comes about that their vascular and nervous systems are so nearly identical.

Several observers have laid stress upon the occurrence of cells upon the surface of the cementum, deep down in the tooth sockets, which are unlike osteoblasts but are obviously epithelial cells. It is claimed by von Brunn that the epithelial sheath of Hertwig from the enamel-organ extends far below the region where enamel is to be formed, and that it is, in fact, co-extensive with the dentine, thus necessarily intervening between the dentine and the cement-forming tissue. He describes the connective tissue bundles as growing through it to attach themselves to the dentine, and thus cutting up the remains of the enamel-organ into small isolated groups of cells, the epithelial *débris* or rests of Malassez, which are to be found here and there in the adult alveolo-dental periosteum (Fig. 90).

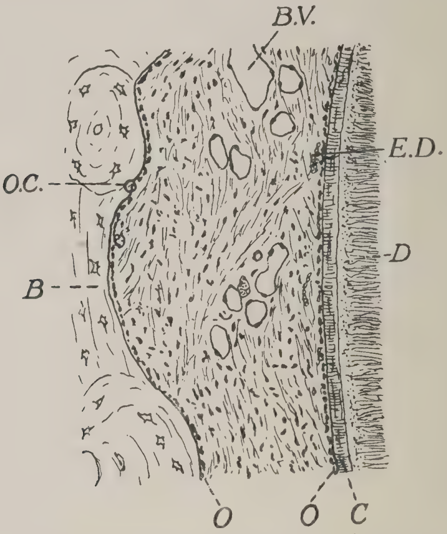

Fig. 89.—Vertical section of the periodontal membrane. *D* = Dentine. *C* = Cementum. *E.D.* = " Epithelial *débris* " of Malassez. *B.V.* = Blood vessel. *O.C.* = Osteoclast. *B* = Bone of alveolar process. *O* = Osteoblast.

Black described, in the sheep, another type of cells which he believed to be lymph cells lining lymph canals ; these are always found close to cementum. He believed also, as corroborative of this view, that he had been able to trace pus infiltration along these chains of cells. He (1899) still adhered to the idea that the accumulations of cells of epithelial character found deep down in the socket are not the remains of the epithelial sheath of Hertwig, but are really glandular structures. He describes them as winding about and branching in every direction, and gives a diagram of their arrangement as seen in a perspective longitudinal view of the membrane, constructed from a number of sections. This diagram is eminently suggestive of their being the remains of the epithelial sheath which has become fenestrated like the spent tooth band (p. 143), and after careful study of his text and figures it appears to the author that the attribution to them of glandular nature rests upon the slenderest foundation.

The human tooth is connected with the living organism very intimately, even though its special tissues are extra-vascular. For blood vessels and nerves enter the pulp in abundance; and the dentine is organically connected with the pulp by the dentinal fibrils.

A favourable place in which to study the nature of the alveolo-dental membrane is the rapidly changing tooth of the crocodile. In it the membrane is very thick, and its bundles of connective tissues very apparent.

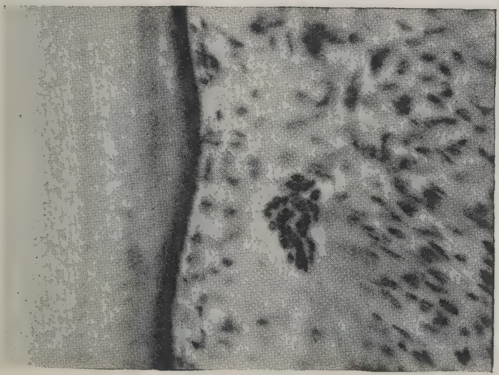

Fig. 90.—Photomicrograph of vertical section of cementum and periodontal membrane, showing prominent group of epithelial cells. (C. B. H.)

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CHAPTER V.

THE DEVELOPMENT OF THE TEETH.

THE development of the teeth is a process which, while subject to modifications in the different groups of vertebrates, nevertheless retains in all of them certain essential characters, so that it becomes possible to embody its main features in a general account.

Prior to the commencement of any calcification there is always a special disposition of the soft tissues at the spot where a tooth is destined to be formed; and the name of "tooth-germ" is given to those portions of the soft tissue which are thus specially arranged. A part only of the soft structures making up a tooth-germ becomes converted into the dental tissues by a deposition of salts of lime within their own substance. The details of this conversion can be better discussed at a later page; for the present it will suffice to say that the three principal tissues, namely, dentine, enamel, and cementum, are formed from distinct parts of the tooth-germ, and that it is customary to speak of the enamel-germ and the dentine-germ. The existence of a special cement-germ is asserted by Magitot, but as yet his description awaits confirmation.

The account of the development of the teeth given in the following pages (based, in the case of man and mammals, upon the researches of Kölliker, Thiersch, Waldeyer, Röse, Leche, and others; in the case of reptiles and fishes, upon those of Huxley, Santi Sirena, Hertwig, Tomes, and others) will be found to differ from the older accounts published by that deservedly great authority, Sir Richard Owen. Modern methods of research have made it easy to demonstrate facts heretofore not demonstrable; yet seventy years ago Professor Huxley demonstrated in a remarkable paper (11) the incorrectness of certain of the theories then promulgated. Of the general accuracy of the following description the author is, however, fully satisfied, and most of the facts may be easily verified by any one desirous of so doing.

True tooth-germs are not formed quite upon the surface of the jaw, but are situated at a little distance beneath it, in many animals ultimately coming to lie at a considerable depth.

A few exceptions to this statement may be cited. The dermal denticles of sharks, which are homologous with their teeth, are formed near to the surface, as are the first teeth of *Triton* (newt), according to Röse, who says that they sink in subsequently. Röse also appears to regard the tooth-germs of some osseous fish as in the same category, but Leche dissents from this, and, indeed, considers Röse's view as merely a question of terms.

Tooth-germs consist in the first instance of two portions, and two only, the enamel-germ and the dentine-germ ; and these are derived from distinct sources, the former being a special development from the epithelium of the mouth and consequently epiblastic, the latter from the more underlying parts of the submucous tissue, and therefore mesoblastic. Other things, such as a tooth capsule, may be subsequently and secondarily formed, but in the first instance the tooth-germ consists of an enamel-germ and a dentine-germ only, and the simplest tooth-germs may never develop any additional parts. The existence of an enamel-organ in an early stage is therefore perfectly independent of any subsequent formation of enamel. But even before this was known the author had shown that it may be found in the germs of teeth which have no enamel.

That part of the tooth-germ destined to become dentine is often called the dentine-papilla, having acquired this name from its papilliform shape ; and in a certain sense it is true that the enamel-organ is the epithelium of the dentine-papilla. Yet, although not absolutely untrue, such an expression might mislead by implying that the enamel-organ is a secondary development, whereas its appearance is antecedent to that of the dentine-germ. The most general account that one can give of the process is that in the future tooth-bearing part of the jaw there is an involution of the superficial epithelium, or rather of its deeper layer. This downward growth consists of a double layer of cells, which in section has somewhat the appearance of a simple tubular gland.

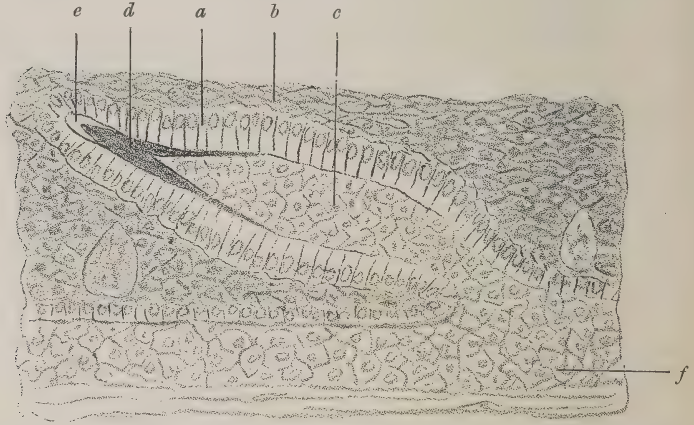

FIG. 91.—Developing dermal denticle of a Selachian. (After Hertwig.) *a.* Enamel cells. *b.* Epithelium of surface. *c.* Dentine-papilla. *d.* Formed dentine. *e.* Formed enamel. *f.* Cells of the mesoblast.

At certain points a further development of the epithelium takes place, forming enamel-organs, beneath each of which a specialisation of the mesoblastic tissue goes on, forming the dentine-papilla. The details of this process vary in different creatures.

In Mammalia the earliest changes which will ultimately result in the formation of a tooth are traceable at a very early period. In man these occur before ossification has set in, while the lower jaw is represented solely by Meckel's cartilage, as yet not fully formed and imbedded in embryonic tissue, and while the lateral processes, which will ultimately become the maxillary bones, have only just reached as far as the median process or premaxillary bone. That is to say, about the fortieth or forty-fifth day of intra-uterine life, in the situation corresponding to the future alveolar border, there appears in transverse sections an ingrowth of epithelium extending along the whole length of the jaw, rounded on its deeper aspect. This rapidly extends more deeply into the subjacent mesoblastic tissue, so that it comes to appear in section like a tubular gland, although it is in reality a continuous sheet or lamina of epithelium,* the primitive tooth-band or " Zahnleiste " of German authors.

In some animals, *e.g.*, in artiodactyles, and in some marsupials, there is a considerable heaping up of epithelium over the tooth-band (see Fig. 94). Leche takes exception to these figures as not representing an occurrence typical of all mammals at this early stage. [Bolk (3) also takes the same view and states definitely that it is never met with in human embryos.] Nevertheless, it is a condition which is present to a greater or less degree in many mammalian embryos.

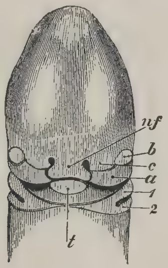

FIG. 92.—Embryo at end of fifth week. 1, 2. First two visceral arches. *a.* Maxillary process. *t.* Tongue. *b.* Eye. *c.* Lateral naso-frontal process. *nf.* Median naso-frontal process. (After Carpenter.)

To this heaping up of epithelium (Zahnwall) over the position of the ingrowth, though it occurs in man but to a very slight extent, and in only a part of the jaw, Röse attaches importance, as he considers it to be a remnant of free tooth formation in the epithelium such as occurs in the larval teeth of fishes and amphibians.

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* The epithelium having been removed by maceration or by keeping a specimen in dilute spirit, a groove would result, and this is probably what was seen and described by Goodsir as the " primitive dental groove " ; but, as the student will gather from the text, there is at no time any such thing as a deep open groove like that described by him, unless it results from maceration and consequent partial destruction of the specimen.

About the same time that the tooth-band becomes differentiated, an ingrowth of epithelium takes place all around the outer surfaces of the jaws in the situation which is to be occupied by the vestibulum oris, or groove between the lips and cheeks and the jaws, the future history of this ingrowth being that it widens out and the cells which fill its interior atrophy, so as to leave an open groove.

To this ingrowth the Germans give the name of "Lippenfurche," a name for which the English equivalent "Lip-furrow" may be substituted. A certain amount of difference of opinion as to its exact origin exists. Röse considers that the tooth-band and the lip-furrow have a common origin, and that the primitive tooth-band splits longitudinally, its outer division forming the lip-furrow and its inner division being the true tooth-band, whilst Baume holds that the true tooth-band originates in the lip-furrow. On the other hand, Leche, an equally careful observer, considers that neither of these statements has a general applicability, and that the lip-furrow and the tooth-band have a simultaneous and independent origin, at all events in many animals.

The question does not appear to be of any paramount importance, as, even taking Röse's own figures, the divarication of the two epithelial inflections takes place at a time when neither is advanced beyond the merest beginnings.

The successive stages of tooth development have been made more intelligible by the researches and models of Röse, who has made use of Born's method of modelling. A complete series of sections of uniform and known thickness are made and photographed or traced with a camera lucida to the same scale. The outlines of every fourth or fifth section are then copied on to tracing-paper affixed to sheets of wax, the thickness of the wax bearing a definite relation to the magnification of the sections and to the thickness and number of those represented by each sheet. The wax is then cut out round the line of the tracing, and the various sheets of wax welded together.

It is obvious that if the wax sheets are of a thickness exactly proportionate to the thickness and number of sections to which each corresponds, and if the sheets so cut out are placed with their flat surfaces together, they will, after being united by running a hot spatula along their edges, exactly represent, on a magnified scale, the object in the solid.

But it is of course impossible to represent thus more than one set of structures at a time, though, by making a tracing round any set that may be selected, a solid model of that structure is the result.

The result of a study of models brings into prominence the following facts : the original inflection (tooth-band, epithelial lamina, or Zahnleiste) at an early stage appears, according to Röse, to divide into two portions, one of which, the outer, runs nearly perpendicularly outwards from the jaw, and is ultimately connected with the formation of the lip-furrow, whilst the inner, with which the reader is more immediately concerned, passes into the tissues beneath, with a slight inclination towards the middle line.

This stage is reached in the human embryo about the forty-eighth day; then near to, but not quite at, the free edge of the tooth-band small club-shaped thickenings appear at each point where a tooth is about to be formed. Soon each cellular accumulation assumes a bell shape, into the concavity of which a papilla-like specialisation of the submucous tissue grows.

It is to be particularly noted that this formation of bell-shaped future enamel-organs is not at the free edge of the tooth-band or dental lamina, but only very near to it, so that the margin of the band is free to go on growing past them, deeper into the submucous tissue, as may be seen in the foregoing diagrams taken from Hertwig (9). It is from this further growing part of the tooth-band that the enamel-organs of successional teeth, whether one or more, will ultimately be derived. Thus the enamel-organs develop from the labial side of the tooth-band and not from its lower free extremity.

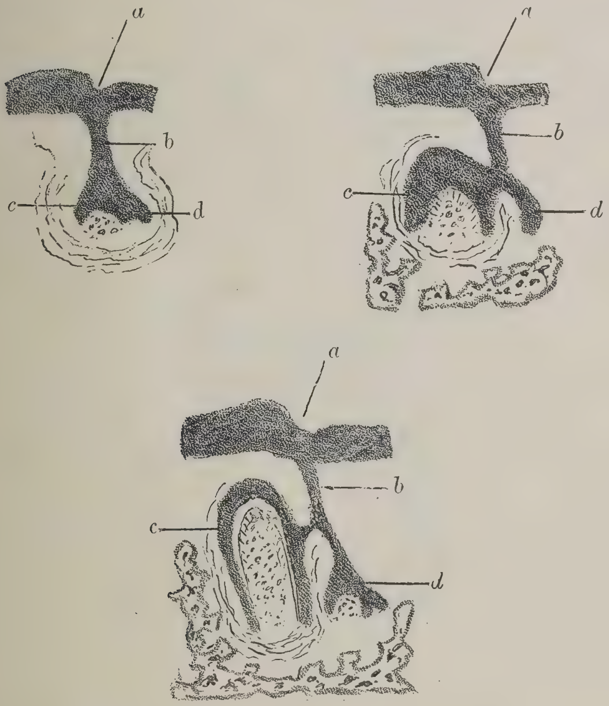

Fig. 93.—Three stages in the development of the human tooth-germ. The right-hand side of the figure is the lingual, or that towards the middle line. (After Hertwig.) *a*. Primitive dental furrow (the existence of which is doubtful). *b*. Tooth-band in section. *c*. Enamel-organ of first tooth. *d*. Free end of tooth-band, to the inner side of which are formed the enamel-organs of successional teeth.

When the bell-shaped cap which constitutes the enamel-organ begins to form, it is, of course, somewhat crescentic when viewed in section. The inner horn of the crescent is formed to some extent by the terminal end of the tooth-band, while the outer bends outwards from it a little way up, and the whole is not detached to any appreciable degree by constriction from the general body of the tooth-band ; so that for a little time it looks as if the end of the tooth-band were wholly used up in its formation. The band begins to grow rapidly beyond it (Fig. 93), and from this further prolongation any successional teeth-germs, if there are to be any, will be formed.

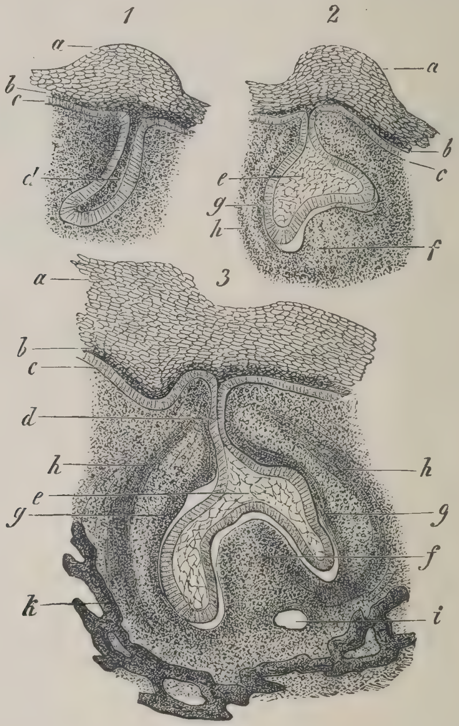

FIG. 94.—Three stages in the development of a mammalian tooth-germ. (After Frey.) *a.* Oral epithelium heaped up over germ (Zahnwall). *b.* Younger epithelial cells. *c.* Deep layer of cells, or rete Malpighi. *d.* Inflection of epithelium for enamel-germ (Zahnleiste). *e.* Stellate reticulum. *f.* Dentine-germ. *g.* Inner portion of future tooth-sac. *h.* Outer portion of future tooth-sac. *i.* Vessels cut across. *k.* Bone of jaw. These figures are not quite complete, in that they do not show the continuation of the tooth-band beyond and to the lingual side of the tooth-germs, and in that the Zahnwall is but a doubtfully typical structure.

The tooth-germs, as has been stated, are formed always upon the outer or labial aspect of the tooth-band, which is inclined inwards towards the middle line ; hence it follows that when a tooth-germ lies upon the lingual side of another, it necessarily belongs to a later generation of teeth, and *vice versâ*. The position of the tooth-germs with relation to the tooth-band has been aptly compared to "swallows' nests built against a board."

Some writers attach so much importance to the growth of the free edge of the tooth-band beyond and to the lingual side of the forming tooth-germ that they consider that wherever it exists there is a possibility, a potentiality, of a further generation of teeth being developed.*

While the tooth-band is continuous round the whole jaw, its further development, resulting in the formation of tooth-germs, takes place at detached points only, where teeth are going to be formed. These appear about the ninth week of intra-uterine life in man.

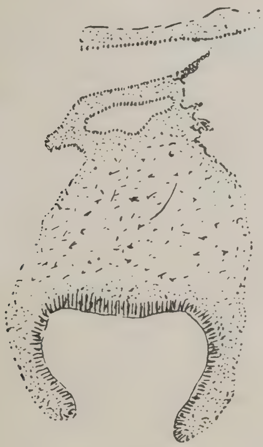

FIG. 95.—Enamel-organ, showing tunnel. (After Bolk, Journ. Anat., vol. lv., London, 1921.)

The further development of an individual enamel-organ may now be described. The first result of rapid proliferation of cells is to bring it somewhat into the form of a Florence flask ; then, as the future dentine-papilla becomes more defined and pushes into it, the enamel-organ assumes the form of a bell with a handle, like a dinner-bell, as may be seen in the accompanying figures. At the same time the enamel-organ recedes from the tooth-band, so that it comes to be connected with the latter only by a narrow double line of cells, as seen in section ; this goes on ultimately to the detachment of the enamel-organ from the tooth-band.

[Bolk (³) has recently described certain details in the development of the enamel-organ which have been overlooked hitherto, and to which he attaches very great importance. This writer considers that the dental lamina has a wider significance than is usually attributed to it, since " the gum at the oral surface of the alveolar ridge is produced by it," and he, therefore, prefers to call it the "dento-gingival " sheet.

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* For a full discussion on this point, *vide* Wilson and Hill, Quart. Journ. Micr. Sci., London, 1896.—[ED.]

Dealing principally with the development of the teeth of the Primates, though obtaining confirmation from mammalia generally, he describes stages in the development of the enamel-organ in which the latter is connected with the dental lamina by *two* strands of epithelial cells, a lateral and a median. On the anterior face of the enamel-organ is an indentation which Bolk terms the " *Enamel-niche*," and which he believes to be of universal occurrence. Traced backwards and at a later stage, the posterior wall of the enamel-niche becomes perforated, leading into a tunnel which runs through the posterior half of the enamel-organ (Fig. 95). It is in this position that the double junction of the enamel-organ with the dental lamina is seen, the median wall or strand (*inner enamel-band*) being formed by the dental lamina itself, and the lateral (*outer enamel-band*) formed by a thin layer of epithelial cells.

These structures, he states, are more difficult to see in the molar region owing to the superficial position of the developing teeth, and also because here the enamel-niche may occur on the posterior face with the canal occupying the posterior half of the enamel-organ, instead of the reverse condition. The existence of this enamel-niche appears to have been noted simultaneously by Ahrens (1) and subsequently confirmed by Sicher (15) in the mole.

With the gradual enlargement of the enamel-organ in a buccal direction the tunnel becomes widened and alters its relative position, usually more to the lingual side of the enamel-organ.

The existence of the enamel-niche is entirely confined to the enamel-organ of the mammals.]

Leche distinguishes three stages in the development of an enamel-organ, which are of use in describing rudimentary organs which do not proceed to full development, by giving a definite indication of the stage to which they have gone on.

1. The bud-shaped germ.
2. The bell or cap-shaped germ without differentiation of its constituent cells.
3. The bell-shaped germ with differentiation of its outer and inner epithelia, or complete enamel-germ.

According to Leche, the detachment of the formed enamel-organ from the tooth-band is the necessary accompaniment of the formation of the next new successional tooth-germ, and so long as the tooth-band retains its connection with the surface epithelium and has a down-growth beyond the last-formed tooth germ, so long is there a possibility of the development of more generations of teeth. He holds, therefore, that in a region where these appearances obtain it is a fair inference that tooth-building is not yet concluded.

In the enlargement which constitutes the young enamel-organ (bud-shaped stage) the cells upon the periphery are columnar, polygonal cells occupying the central area of the enlargement. Very soon the terminal enlargement, as it grows more deeply into the jaw, alters in form; its base becomes flattened, and the borders of the base grow down more rapidly than the centre, so that its deepest portion presents a concavity looking downwards; it might be compared to a bell suspended from above by the thin cords of epithelium which still connect it with the epithelium of the surface, or it might in section be described as crescentic, the horns of the crescent being long, and pointing downwards. Coincident with the assumption of this form by the enamel-germ is the appearance of the dentine-germ; but it will facilitate the description of the process to pursue the development of the enamel-organ to a further stage.

A shallow furrow (the primitive dental furrow) has by this time appeared on the free surface of the epithelium in the mouth, which corresponds with the situation of the tooth-band (cf. Fig. 93). The cells on the periphery of the enamel-organ remain prismatic or columnar, but those in its centre become transformed into a stellate network, in which conspicuous nuclei occupy the centre of ramified cells, the processes from which anastomose freely with those of neighbouring cells (see Fig. 103). This conversion of the cells into a stellate reticulum is most marked quite in the centre of the enamel-organ. Near to its surface the processes of the cells are short and inconspicuous, and the whole process strikingly recalls the phenomena of colloid degeneration as observed in certain tumours.

The transformation of the cells occupying the centre and constituting the bulk of the enamel-organ into a stellate reticulum goes on progressing from the centre outwards, but it stops short of reaching the layer of columnar cells which constitute the surface of the enamel-organ, next to the dentine-papilla. A narrow layer of unaltered cells remains between the stellate cells and the columnar enamel cells and is known as the "stratum intermedium."

[Bolk's account differs in certain details from the description just given of the formation of the stellate reticulum.

According to this writer the formation of the stellate tissues commences, not in the centre, as usually described, but from two points, a lingual and a buccal, these being separated by a nuclear layer passing from the apex of the developing tooth to the outer enamel epithelium, the point of junction with the latter being the enamel-navel. This he calls the "*enamel-septum*," and which he states is deficient in the posterior part of the enamel-organ. The cells and nuclei of the septum elongate vertically, but never become converted into stellate tissues. In *Phascolarctus cinereus* blood vessels which may be seen entering at the navel and passing down the enamel-septum are distributed among the cells of the "stratum intermedium."

At a later stage, the septum becomes deficient anteriorly as well as posteriorly, remaining only as a central conical cord of cells. The condition was noted by Renaut in 1897 and described as the "*cône adamantin directeur*." In monocuspidate teeth this septum passes at its deeper end from the apex of the cusp, but in the molars from the furrow intervening between two cusps, or more rarely is placed so excentrically as to appear to have no definite topographical relationship with the cusps. This septum, according to Bolk, is only to be found in developing mammalian teeth.

As will be seen in a subsequent chapter, Bolk attaches considerable importance to these new facts in the history of the enamel-organ.

That this enamel-septum does exist cannot be doubted. Attention was drawn to it in *Macropus billardieri* in 1911 (*vide* Fig. 203, p. 334) by Hopewell-Smith and Marett Tims, who regarded it as of exceptional occurrence, and it is difficult to believe that so striking an appearance can have been so generally overlooked if its presence is so constant and so universal as Bolk claims it to be.]

Leon Williams, however, does not consider that the cells have changed into a stellate form, but that this stellate appearance is an intercellular substance, from which the cells have been washed out. He states that the spaces are not empty in preparations rapidly fixed in Fleming's or Hermann's solution and examined in glycerine, but that the contents are always lost in balsam preparations. Williams is, so far as is known, the first to have observed and described the contents of these spaces; but the author does not think that his observation is at all inconsistent with the view that the cells have undergone a sort of colloid degeneration, for it is characteristic of colloid changes for the nucleus to be pressed out against the periphery, and as the change goes on in a myxoma, or in colloid degeneration of a cancer, a stellate-looking tissue comes to be formed by the squeezing outwards of the nucleus and approximation of the walls of neighbouring cells, whilst the colloid material is frequently lost from the interior in cutting the section.

Eve (6) has also shown that in certain cystic tumours of the jaws the epithelium which enters into them undergoes a sort of colloid degeneration, resulting in appearances almost precisely resembling the stellate tissue of the enamel-organ. The cells become much enlarged, and the nuclei pressed against the cell-walls. The protoplasm of the individual cells then becomes merged into a general mass, but the nuclei with portions of the cell-walls attached to them remain, so that the resultant tissue has much the appearance of flattened cells with processes. In some places a drop of colloid substance forms within the individual cell, and the protoplasm is expanded out into a thin layer, so that the nucleus is pressed against the cell-wall, thus producing the characteristic signet-ring appearance. Similar forms are to be found in enamel-organs. Thus a cystic epithelium, probably identical in its origin with the enamel-organs, may undergo a degenerative change, which brings it into close similarity with this part of the enamel-organ.

Thus far all the cells constituting the periphery of the enamel-organ are alike: they are columnar or prismatic; but from the time of the appearance of the dentine-papilla those which come into relation with it become much more elongated and greatly enlarged, while those round the outer surface constituting the "external epithelium" of the enamel-organ do not enlarge; indeed, according to some authors, they even commence to flatten and to atrophy at this early period. The cells which lie like a cap over the dentine-germ or "papilla" as they elongate, and their nuclei recede towards their extremities, take on the character to be presently described as belonging to the "enamel cells" (enamel epithelium, internal epithelium of the enamel-organ, adamantoblasts, or ameloblasts).

The enamel-organ, then, consists (proceeding from without inwards) of an " external epithelium," a " stellate reticulum," a " stratum intermedium," and an " internal epithelium," the external and internal epithelia being continuous at the edges or base of the enamel-organ, while at its summit the external epithelium remains still, through the medium of the " neck of the enamel-organ," in continuity with the cells of the tooth-band, and through them with the cells of the " stratum Malpighi."

Thus the enamel-organ is entirely derived from the oral epithelium, with which, by means of its " neck," it long retains a connection, so that it, and whatever products it may afterwards give rise to, are obviously to be regarded as " epithelial structures," and epiblastic in their origin. But it is the enamel-organ alone which is directly derived from the epithelium ; the origin of the dentine-germ is quite distinct.

[In connection with the enamel-organ, Bolk describes an " *accessory band* " of epithelium, an epithelial sheet, situated buccally to the dental lamina and growing backwards concurrently with it. This accessory band has a striking resemblance to the dental lamina, from which in certain situations it appears to take origin, in others from the superficial epithelium, but it has nothing to do with the development of the mammalian tooth. At its deeper end this band becomes branched opposite to each developing tooth and often, according to Bolk, gives the appearance of a commencing enamel-organ, but without any condensation of mesoblastic tissue to indicate the formation of a dental papilla. In reality this is a gland developed in connection with each tooth. Its glandular nature is stated to be well seen in the mole. A similar condition is well known to exist in reptiles, and Bolk homologises the mammalian " accessory band " with the " glandular band " of the reptiles. It is to this band that he would refer all the evidences of a pre-milk dentition which previous observers have described. These are not to be confused with the so-called glands of Serres. Reference will again be made to this subject in a subsequent chapter.]

Degenerative changes begin to appear in the common tooth-band so soon as the tooth-germs are well on their way in their development, and fenestrations begin to form in it, so that, instead of being a flat and complete sheet, it becomes a cribriform sheet ; hence a fallacious appearance of its being broken up and no longer continuous with the surface results when individual sections are viewed, it often happening that the plane of the section coincides with one of the perforations in the sheet.

But, as has already been hinted, this change does not go on uniformly everywhere in the dental lamina, but only where its work is nearly accomplished ; thus at the back of the mouth, where more teeth have to be developed, it is still a complete sheet, and to the lingual sides of the milk teeth, where the successional teeth are to be formed, it also remains complete and continues to grow.

The same sort of change takes place in the necks of the enamel-organs, and ultimately these, as well as the dental lamina itself, break up into isolated islands of epithelium, which sometimes seem to proliferate a little, and constitute the little masses of epithelium known as the "glands of Serres."

It is possible that these little nests of epithelium may be the site of certain new growths which sometimes arise in the jaws.*

So far the ingrowth of the epiblastic epithelium into the mesoblastic tissue beneath it has been described, but wherever this has gone on to the formation of an enamel-organ, the mesoblastic tissue seems to be stimulated to growth, leading to the formation of the dentine-germ. Leche thinks that the differentiation and crowding of the cells of the mesoblast may be at first merely the mechanical effect of the vigorous ingrowth of epithelium, as he has observed it near to the end of the tooth-band, *i.e.*, at points where tooth-germs are not going to be formed. However that may be, in the embryonic tissue of the jaws, some little distance beneath the surface, and at a point corresponding to that ingrowth of cells and subsequent enlargement of the same which goes to form the enamel-organ, appears the first trace of a dentine-germ.† This is at first a mere increase in the opacity of the part, without any visible structural change, and it occupies the concavity of the enamel-organ. Thus the dentine-germ appears early, indeed almost simultaneously with the formation of the definite enamel-organ, but the latter is far in advance of the former in point of structural differentiation, and the earliest changes resulting in the formation of the enamel-organ are strikingly visible before a dentine-germ can be discovered. Hence it has been suggested that the enamel-organ governs and determines the ultimate form of the tooth. According to Dursy (5), the dark halo which becomes the dentine-bulb is, like the inflection of epithelium which forms the enamel-germ, continuous all round the jaw, while eventually it develops into prominences at the points corresponding to the enamel-germs of future teeth, and atrophies in their interspaces.

From the base of the dentine-bulb prolongations pass outwards and slightly upwards, so that they in a measure embrace the free edge of the enamel-organ, and at a somewhat later period they grow upwards till they fairly embrace the whole enamel-organ. These prolongations are the rudiments of the dental sac or capsule. In their origin, therefore, the dental sac and the dentine-organ are identical, and spring from the submucous tissue; they contrast with the enamel-organ, which, as before said, is derived from the oral epithelium.

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* For a further consideration of epithelial nests in connection with developing teeth, *vide* p. 326.

† The term "dental papilla," although eminently convenient, is associated with an erroneous feature of the older views upon tooth development; where it is employed in the following pages, the student must guard against the misconception that free papillæ at any time exist in any animal.

To recapitulate briefly the facts which are now established beyond all question, the early mammalian tooth-germ consists of three parts, one of which, the enamel-organ, is derived from the epithelium of the surface; the other two, the dentine-organ and the dental sac, originate in the midst of solid embryonic tissue at a distance from the surface; the one is ecderonic or epiblastic, and the other enderonic or mesoblastic. The enamel-organ is formed by a rapid increase of cells near to the bottom of a process which dips in from the stratum Malpighi of the oral epithelium; the dentine-germ and the dental sac are formed in close continuity to this enamel-organ from the submucous tissue.

If there were a "basement membrane" demonstrable in the mucous tissues at this early period (which there is not) the enamel-organ and the dentine-organ would lie upon the opposite sides of it.

Malassez insists much upon the significance of remnants of epithelium left after the atrophy of the enamel-organ; some of these he believes that he has found in the alveolo-dental membrane (Fig. 89). This is confirmed, as to developing teeth, by von Brunn (4), who states that in rodents the enamel-organ extends far down, in fact, the whole length of the roots, and figures the fibres of the alveolo-dental periosteum as growing through it to take hold of the cementum; it seems possible that these cells are the same which Black and Xavier Sudduth consider to be portions of a lymphatic system.

Before leaving the subject of the enamel-organ, it may be mentioned that several writers, notably von Brunn and Ballowitz (2), hold that the primary function of the enamel-organ is that of determining the form of the future tooth, even going so far as to suggest that its calcification to form enamel is in some animals a secondary function, taken on later. In support of this contention they urge that enamel-organs are universal, even where no enamel is found; and that in teeth where there is a partial investment of enamel on the dentine the enamel-organ extends far beyond the enamel limits.

Moreover, they trace extensions of the enamel-organ right down to the bottom of the roots in those teeth where the whole crown only is invested with enamel. Indeed, von Brunn says that it is to be traced between the roots of a three-rooted tooth, so that it may be compared to something enveloping a three-legged stool, creeping round its edges, its under-side, and finally growing down as an envelope to each leg. Its presence is confirmed by Röse, who says that so soon as its increase downwards ceases, so does that of the dentine. Thus von Brunn holds that everywhere where dentine is to be formed there is an antecedent "form-building" investment of enamel-organ; and to this, and not to any retrogression, he would attribute the enamel-organ of Edentata.

But whatever may be thought as to its "form-building" functions, recent researches into aborted and rudimentary teeth of mammals render it quite certain that in that class at all events a complete dentition of enamelled teeth was the rule, and that those which have lost, or partly lost, their teeth have arrived at this state by degeneration, so that it seems a fair inference to suppose that where enamel is absent, that also is in the nature of a degeneration.

The development of the teeth in lower vertebrates has, as already mentioned, very much that is common to them and to the higher, the principal difference lying in the arrangements for succession.

Elasmobranch Fishes.—If a transverse section through the jaw of a dog-fish (*Scyllium canicula*) be examined, it will be found that the developing teeth lie upon the inside of the cartilaginous jaws, the youngest being at the bottom (Fig. 96). Progressing upwards, each tooth is more fully calcified till, at the border of the jaw, are situated the functional organs and those teeth whose period of greatest usefulness is past and which are about to be cast off in the course of that slow rotation of the whole tooth-bearing mucous membrane over the border of the jaw which is constantly going on.

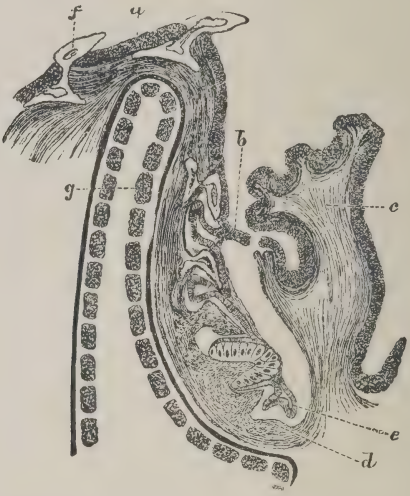

Fig. 96.—Transverse section of lower jaw of a dog-fish. *a*. Oral epithelium. *b*. Oral epithelium passing on to flap. *c*. Protecting flap of mucous membrane (thecal fold). *d*. Youngest dentine pulp. *e*. Youngest enamel-organ. *f*. Tooth about to be shed. *g*. Cartilage of jaw. Note the great development of enamel cells over the third papilla from the base.

In this figure four teeth advanced in calcification are represented, while beneath them are three tooth-germs in earlier stages of development. Of the former two only are fully protruded through the epithelium, the third being in part covered in; the remaining teeth are altogether beneath the surface of the epithelium, and therefore shut off from the cavity of the mouth, if the soft parts be all *in situ*.

All the teeth not fully calcified are covered in and protected by a reflexion upwards of the mucous membrane (c in the figure), which serves to protect them during calcification.

But although this may be termed a fold reflected upwards, it is not, as was supposed by Sir Richard Owen, a free flap, detached from the opposite surface on which the teeth are developing; there is no deep open fissure or pouch running round inside the jaw, as would in that case exist, and the epithelium does not pass down on the one side to the bottom of such fissure, and then ascend upon the other as a distinct layer. On the contrary, we have here that inward-growing inflection of epithelium known as the "tooth-band" (Zahnleiste). Although the fold is very easily torn away from the tooth-germs which it covers in, yet in the natural condition it is attached, and there is no breach of surface; the epithelium of the jaw is seen in the figure, in which the epithelial layer is represented as broken just at the point between the third and fourth teeth, where the tooth-band dips in.

The conditions met with in the Elasmobranch fishes are peculiarly favourable for the determination of the homologies of the several parts of the tooth-germ and of the formed tooth.* At the base of the jaw, where the youngest tooth-germs are to be found, the tissue whence the dentine-papillæ arise blends insensibly with that making up the substance of the thecal fold on the one hand, and, on the other, with that clothing the concavity of the jaw and giving attachment to the teeth.

No sharp line of demarcation at any time marks off the base of the dentine-papilla from the tissue which surrounds it, and from which it springs up, as would be the case in mammalian or reptilian tooth-germs; all that can be said is, that the dentine-germs are cellular, the cells being large and rounded, while in the rest of the mucous membrane the fibrillar elements preponderate, so that it passes by imperceptible gradations into the densely fibrous gum, found on the exposed border of the jaw.

The dentine-germs, and consequently the dentine, are indisputably derived from the connective tissue of the mucous membrane immediately subjacent to the epithelium, nor can it be doubted that the enamel-organs are simply the modified epithelium of that same mucous membrane.

Of course there is nothing new in this conclusion, which had been already arrived at by the study of other creatures, but the sharks happen to demonstrate it with more clearness than those other animals in which the original nature of the process is more or less masked by the introduction of further complexities. Hence it is worth while to study carefully the relations of the epithelium constituting the enamel-organs with that of the surface of the mouth.

As has been already mentioned, in the normal condition of the part there is no deep fissure on the inner side of the jaw, but the epithelium passes across (from the interspace between the third and fourth teeth in the figure) on to the protecting fold of mucous membrane (*c* in Fig. 96). The epithelium in this situation does not, then, consist simply of one layer going down on the one side and covering the tooth-germs, and then reflected up at the bottom to coat the inner side of the thecal fold, but it is an inflexion of the deep layer of a tooth-band ; it is termed the " enamel-organ " because over the tooth-germs these epithelial cells assume a marked columnar character, and are very different in appearance from the epithelium elsewhere, especially at that stage during which enamel formation is most active.

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* Compare the description of the dermal spine (pp. 3 and 134).

The terminal portion of this tooth-band runs beyond the youngest enamel-germ, which forms a bell-like cap over the eminence of connective tissue which constitutes the earliest dentine-germ, and in section is of the form shown in the figure. The surface next to the dentine-papilla consists of elongated columnar cells, with nuclei near to their middles, while the rest of its substance is made up of much smaller cells, some of which have inosculating processes, so that they constitute a sort of finely cellular connective tissue, very different in appearance from anything met with in mammalian enamel-organs. It is sufficiently consistent to keep up the continuity of all the enamel-organs, even when displaced in cutting sections, so that the whole might almost be described as forming one composite enamel-organ. The columnar cells already alluded to invest the whole surface which is directed towards the forming teeth, but they atrophy somewhat in the interspaces of the tooth-germs.

Before proceeding further in the description of the development of the tooth-germs, it will be well to refer again to an earlier stage in the growth of the dog-fish, in which the relation subsisting between the teeth and the dermal spines is still well seen.

On the lower jaw of the young dog-fish there is no lip ; hence, as is seen in the figure, the spines which clothe the skin come close to the dentigerous surface of the jaw.

Although there are differences in form and size, a glance at the figure will demonstrate the homological identity of the teeth and the dermal spines. As the dog-fish increases in size, this continuity of the teeth with the dermal spines on the outside of the head becomes interrupted by an extension of the skin to form a lip. This happens earlier in the upper jaw than in the lower, and at first the spines are continued over the edge and the inside of the newly formed lip ; from these situations, however, they soon disappear. In structure, the teeth and the dermal spines are, in many species, very closely similar ; the latter are, however, much less often shed and reproduced, so that it is less easy to find them in all stages of their growth ; the author believes, however, that they follow a course essentially similar to that of the teeth.

It is stated by Gegenbaur (7) that in *Selachia* the mucous membrane of the mouth is clothed with spines of a structure similar to that of the teeth, and that these spines are often limited to particular regions, extending back as far as the pharynx, these same regions in Ganoid and Osseous fishes being occupied by conspicuous teeth; and Hertwig (9) has shown that the dermal spines are developed in a manner precisely similar to that described in the teeth, save that the germs are even less specialised.

There are certain peculiarities in the enamel-organ of *Selachia*, and also in the dentine-papillæ, which may be more advantageously described in connection with calcification.

Teleostei or Osseous Fishes.—In passing from the consideration of the development of the tooth-germs of Elasmobranch to those of Osseous fishes, the first difference to be noted is this: whereas in the former each tooth-germ was, so far as the enamel-germ is concerned, easily seen to be derived from the general tooth-band, in the latter each enamel-germ apparently often rises independently, and, as it were, *de novo*. At all events, so far as the author's investigations go, no obvious connection between the germs of teeth of different ages is visible; but Heincke (8) says that in the pike new enamel-organs may be derived from older ones.

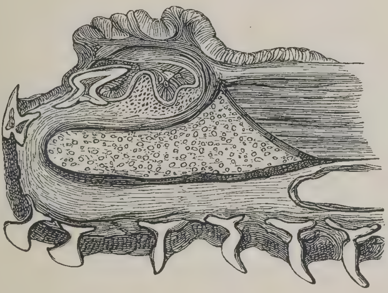

Fig. 97.—Section of lower jaw of young dog-fish, showing the continuity of the dermal spines of the skin under the jaw, with the teeth which lie above and over its end.

This apparently independent origin of an indefinite number of teeth, having no relation to their predecessors, only occurs in the Osseous fish; in them it is likely that the germs so soon become detached that their origin from any common tooth-band is masked. Of the development of the teeth of Ganoid fish next to nothing is known.

The oral epithelium, which varies much in its thickness and in other characters in different fishes, sends down a process which goes to form an enamel-organ, whilst a dentine-papilla in rising up to meet it comes to be invested by it as with a cap. The after-history of the process depends much on the character of tooth which is to be formed. If no enamel, or but a rudimentary coat of enamel, is to be formed, the cells of the enamel-organ remain small and insignificant, as in the mackerel. If, on the other hand, a partial investment of enamel is found upon the perfected tooth, such, for instance, as the little enamel tips upon the teeth of the hake (see Fig. 69), then the after-development of the enamel-organ is very instructive.

Opposite to the apex of the dentine-papilla, where the enamel-cap is to be, the cells of the enamel-organ attain to a very considerable size, measuring about $\frac{1}{400}$ of an inch in length; below this the investing cap of the enamel-organ does not cease, but it is considered to be in a sort of rudimentary condition. Thus, although the enamel-organ invests the whole length of the dentine-papilla, its cells only attain to any considerable size opposite to the point where the enamel is to be formed. The knowledge of this fact often enables an observer to say, from an inspection of the tooth-germ, whether it is probable that the perfected tooth will be coated with enamel or not. In any case an enamel-organ will be there, but if no enamel is to be formed, the individual cells do not attain to any considerable degree of differentiation from the epithelium elsewhere; in other words, the whole enamel-organ will partake of the character of the lower portion of that represented in the figure of the tooth-germ of the eel (Fig. 98).

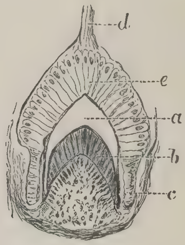

FIG. 98.—Tooth-germ of an eel. *d.* Neck of enamel-organ. *e.* Enamel-cells. *a.* Cap of enamel. *b.* Cap of dentine. *c.* Rudimentary enamel-cells opposite to that part of the dentine-germ where no enamel will be formed.

Although of course there are many differences of detail arising from the very various situations in which teeth are developed in fish, so great uniformity pervades all which have been examined, that the development of the teeth of reptiles may now be considered, merely adding that it is not altogether true to say that the teeth of fish in their development exemplify transitory stages in the development of mammalian teeth.

Amphibia and Reptilia.—So far as the appearances presented by the individual germs go, there are few differences worthy of note to be found by which they are distinguishable from those of either fish or mammals.* The enamel-organ is derived from the tooth-band, and the dentine-organ from the submucous tissue in a very similar manner; nevertheless, there are points in the relation which the successional tooth-germs bear to one another, and to the teeth already *in situ*, which are of some little interest. The constant succession of new teeth met with amongst almost all reptiles renders it easy to obtain sections showing the teeth in all stages of growth. Upon the inner side of the jaw there will be found a region occupied by these forming teeth and by nothing else, which may be called the "area of tooth development"; this is bounded on the one side by the bone and teeth which it carries, and on the other by a more or less sharply defined wall of fibrous connective tissue. In the newt, for example (Fig. 99), to the left of the tooth in use are seen three tooth-sacs, in serial order, the youngest being nearest to the median line of the mouth. As the sacs increase in size they appear to undergo a sort of migration towards the edge of the jaw, while simultaneously new ones are constantly being developed beyond them. The ingrowth of the epithelium is obviously the first step apparent; this ingrowth of a process of epithelium or tooth-band always extends beyond and inside the youngest dentine-papilla, and each new enamel-organ is formed from its side near its growing end. New enamel-organs are therefore not derived directly from the epithelium of the surface, but from the deep end of the tooth-band.

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* According to Bolk, reptiles have in reality no free enamel-organs.—ED.

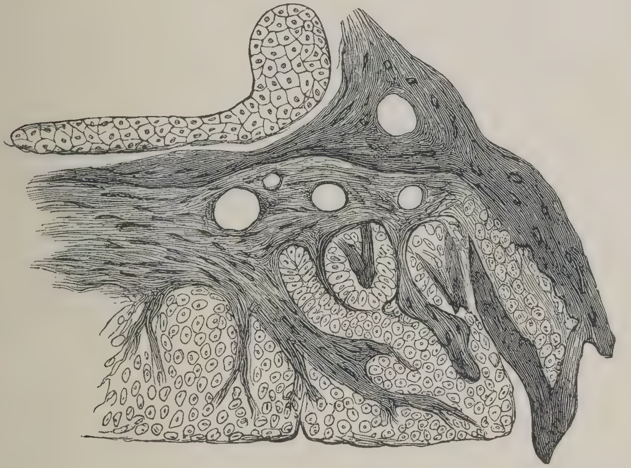

FIG. 99.—Section of upper jaw of *Triton cristatus* (newt). To the inner side of the tooth attached to the bone are three younger tooth-germs.

In this amphibian, the developing teeth spread out for a considerable distance towards the palate, and thus, being free from crowding, the relations of the enamel-organs of three or four successional teeth of serial ages may be studied in a single section; and the arrangement so disclosed may be advantageously compared with that seen in the dog-fish (see Fig. 96).

The tooth-sac of the newt is a good example of the simplest form of tooth-germ, consisting solely of an enamel-organ and a dentine-germ, without any especial investment. The "germ" is wholly cellular, and on pressure breaks up, leaving nothing but cells behind it. The cells of the enamel-organ are large, and resemble those of the eel; the teeth of newts have a partial enamel tip, like those of the fish referred to, but differ from them in being bifurcated, as is very early indicated by the configuration of the enamel-organ.

In the frog there is a peculiarity in the manner in which the two jaws meet, the edentulous lower jaw, which has no lip, passing altogether inside the upper jaw and its supported teeth, and so confining the area of tooth development within very narrow limits. Consequently the author has been unable to satisfy himself whether the new tooth-germs, or rather their enamel-organs, are derived from the primitive tooth-band or spring up *de novo;* analogy would indicate the former, but appearances tend towards the latter supposition.

There is also a peculiarity in the development of the teeth of some reptiles in that the first formed tooth is developed, like the dermal spine of a shark, very close to the surface; in fact, Röse affirms that the first tooth-germ of the crocodile is actually an upstanding papilla.

This, however, is not confirmed by Leche, who says he has never seen an actual free papilla, but he describes and figures in the iguana a little first rudimentary tooth almost in the surface epithelium, and shows that the tooth-band sinks in deeper and deeper by the side of this, till at last the successional teeth are formed as deep as possible on the surface of the jaw-bone, into which, however, they do not pass. For an account of Bolk's views as to the development and succession of the teeth in the Reptilia, the reader is referred to Chapter XI.

In the lizards the new tooth-germs are formed a very long way beneath the surface, so that the neck of the enamel-organ becomes enormously elongated, for the dentine-papilla is, just as in the newt, situated quite at the level of the floor of the area of tooth development. The teeth of the lizards have a more complete investment of enamel, hence the enamel cells are developed upon the side of the dentine-germ to a much lower point than in the newt. The germs also acquire an adventitious capsule, mainly derived from the condensation of the connective tissue around them, which is pushed out of the way as they grow larger. The further progress of the tooth-germ being identical with that of mammalia, its description may be for the present deferred.

Some lizard-like animals, such as *Sphenodon* and the chamæleon, present no evidence of successional teeth being formed, though in them, though acrodont, a "tooth-band" is to be seen to the inner side of the functional tooth (Röse).

In ophidian reptiles (snakes) several peculiarities are met with which are very characteristic of the order. A snake's method of swallowing its food would seem to render the renewal of its teeth frequently necessary; although no data are known by which the probable duration of the life of an individual tooth could be estimated, the large number of teeth which are developing in reserve, all destined to succeed to the same spot upon the jaws, would indicate that it is short.

The author has seen as many as seven successional teeth in a single section, and their arrangement, particularly in the lower jaw, which undergoes great displacement while food is being swallowed, is very peculiar. The numerous successional tooth-sacs, instead of being spread out side by side as in the newt, are placed almost vertically, and in a direction parallel with the surface of the jaw-bone; they are, moreover, contained in a sort of general investment of connective tissue—a species of bag to keep them from displacement during the expansion of the mouth.

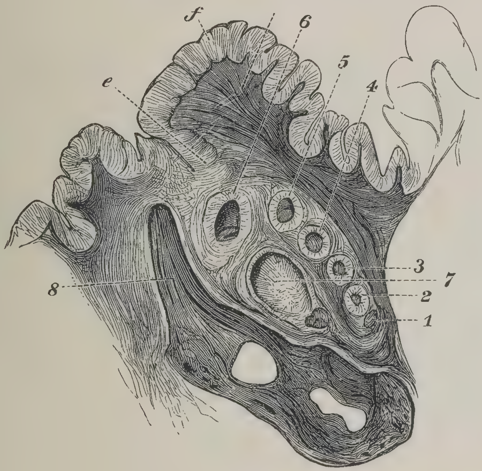

Fig. 100.—Transverse section of the lower jaw of common English snake. *e.* Involution of epithelium. *f.* Oral epithelium. 1, 2, 3, &c. Tooth-germs of various ages. 8. Tooth in place, cut somewhat obliquely, so that its tip apparently falls short of its surface, and does not project above the mucous membrane.

The inward-growing process of oral epithelium enters this collection of tooth-sacs at its top, and may be caught sight of here and there as its prolongations wind their way by the sides of the tooth-sacs to the bottom of the area. Here the familiar process of the formation of an enamel-organ and dentine-papilla may be observed, in no essential point differing from that which is to be seen in other animals.

That the derivation of each enamel-organ is from a part of that of the tooth-band is very obvious; the dentine-organs are formed in relation with the enamel-germs, but apparently independently of one another.

As the tooth-sacs attain considerable dimensions, a curious alteration in position takes place : instead of preserving a vertical position, they become recumbent, so that the developing tooth lies more or less parallel with the long axis of the jaw. The utility of such an arrangement is obvious : were the tooth to remain erect after it has attained to some little length, its point would probably be forced through the mucous membrane when the mouth was put upon the stretch ; but while it lies nearly parallel with the jaw no such accident can occur.

The tooth does not resume the upright position until it finally moves into its place upon the summit of the bone.

As has already been mentioned, there is a well-developed enamel-organ with large enamel cells ; from these a thin layer of enamel is formed, and thus the thin external layer upon the teeth of snakes is probably true enamel, and not, as has been usually supposed, cementum.

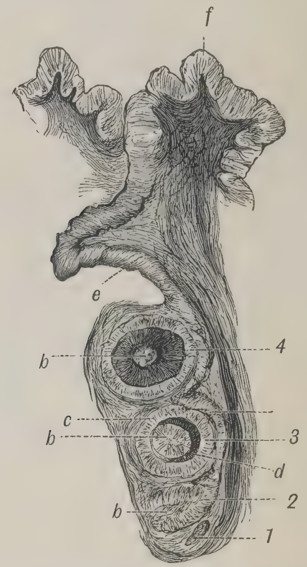

Fig. 101.—Developing teeth of a snake. *f.* Oral epithelium. *e.* Neck of the enamel-organs. *b.* Dentine-pulp. *c.* Enamel cells. *d.* Dentine. 1, 2. Very young germs. 3, 4. Older germs.

The essential feature in the development of reptilian teeth is the indefinitely repeated succession which is the typical condition, though, as already mentioned, in some instances it has become limited or entirely lost ; this seems to have been the case in the most mammalian of reptiles, the Anomodont group. The question of succession has, however, of late years, become so important, and there is such a voluminous literature, that it will require special notice, and a section will be devoted to it.

Mammalia.—The mammalian enamel-organ, as has already been stated, forms a cap-like investment to the dentine-papilla, and it is itself thickest over the apex of the latter, becoming more attenuated as it approaches the base.

It is entirely surrounded by an epithelial layer, which upon the inner surface, applied to the dentine-bulb, consists of very elongated columnar cells, and takes the name of *internal epithelium of the enamel-organ,* and upon its outer surface the name of *external epithelium of the enamel-organ.* The great bulk of the early mammalian organ consists of a stellate tissue (Fig. 102), which passes somewhat abruptly through the medium of a layer of rounded cells, the *stratum intermedium,* into the *enamel cells* (ameloblasts), or *internal epithelium.*

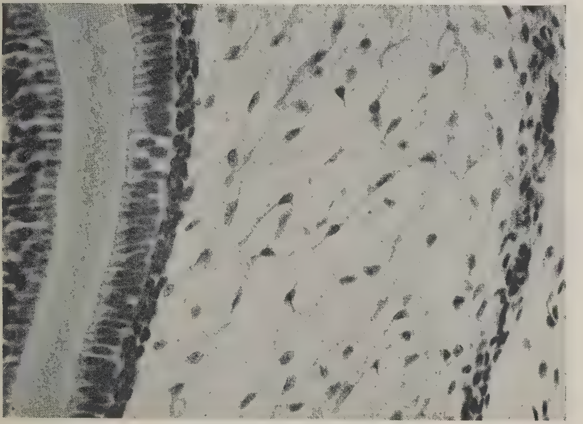

FIG. 102.—Section of developing tooth of kitten, showing odontoblasts, ameloblasts, stratum intermedium, stellate reticulum, and external epithelium of the enamel-organ. (C. B. H.)

The essential portion of the enamel-organ is this layer of "enamel cells," which give rise to the enamel. In lower animals, and most, if not all, reptiles, the whole enamel-organ is represented by little else than this layer of "enamel cells."

The internal epithelium (enamel cells) consists of an exceedingly regular and perfect columnar epithelium, the individual cells becoming by result of their mutual apposition fairly symmetrical hexagons.

They are four or five times as long as they are broad, and the nucleus, which is large and oval, lies near to that end which is farthest from the dentine. According to Waldeyer (16) the sides of the cells only are invested by membrane, the protoplasm being without investment at its two ends. On the other hand, Leon Williams describes structures at both ends of the cells, and calls them the "inner and outer ameloblastic membranes."

Towards the base of the dentine-germ, where the internal epithelium merges into the external epithelium, the cells are not so much elongated, and they pass gradually into the cubical form of these latter cells. At their attached extremities the enamel cells are prolonged into processes which are continuous with the cells of the *stratum intermedium*, so that it has sometimes been concluded that the enamel cells, as they are used up in the formation of enamel, are recruited from the cells of this layer.

The *stratum intermedium* consists of cells intermediate in character between those of the bordering epithelium and the stellate reticulum; they are branched, but less conspicuously so than the stellate cells.

The stellate cells proper are characterised by the great length of their communicating processes, and the interspace of the meshes is occupied by a fluid rich in albumen, so that the consistence of the whole is little more than that of jelly. As the structure in question constitutes the major part in bulk of mammalian enamel-organs, these have been called the enamel jellies, or enamel pulps.

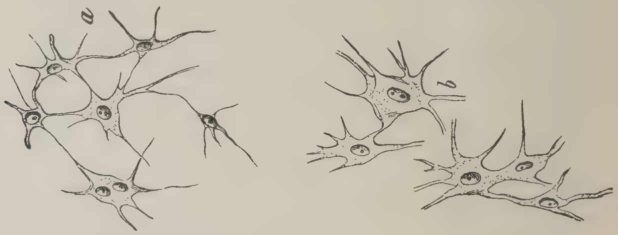

FIG. 103.—Cells of the stellate reticulum of the enamel-organ. (From Frey's "Histology.")

The function and destination of this portion of the enamel-organ is not very clear; enamel can be very well formed without it, as is seen amongst reptiles and fish, and even in mammalia it disappears prior to the completion of the tissue, so that a great deal of the enamel is formed after the external and internal epithelia have come into contact. It has been supposed to have no more important function than to fill up the space subsequently taken up by the growing tooth.

It has been pointed out by Dr. Paul (*loc. cit.*) that this is after all not an unimportant office; the tooth-sac is regular in outline, the apices of the cusps, &c., of the forming tooth very much the reverse; and it is familiar to every histologist that the distribution of the stellate tissue is very unequal, even at the period of its greatest development, the forming tooth in some places coming close to the tooth-sac, in others having a great thickness of stellate reticulum over it. Its thickness bears no relation whatever to the amount of enamel that is to be formed; thus, as just mentioned, over the apices of the cusps it is often almost absent.

The external epithelium of the enamel-organ is composed of cells cubical or rounded in form, and is of little interest save in that it is a matter of controversy what becomes of it. Waldeyer holds to his opinion that, after the disappearance of the enamel pulp and the *stratum intermedium*, it becomes applied to the enamel cells, and on the completion of the enamel becomes cornified and converted into Nasmyth's membrane. Kölliker and Legros and Magitot dissent from this opinion, the latter stating that the atrophy of these cells commences early, and that they actually disappear prior to the complete atrophy of the organ. The external epithelium was seen by Nasmyth, Huxley, and Guillot, but it was not very fully described until investigated by Robin and Magitot.

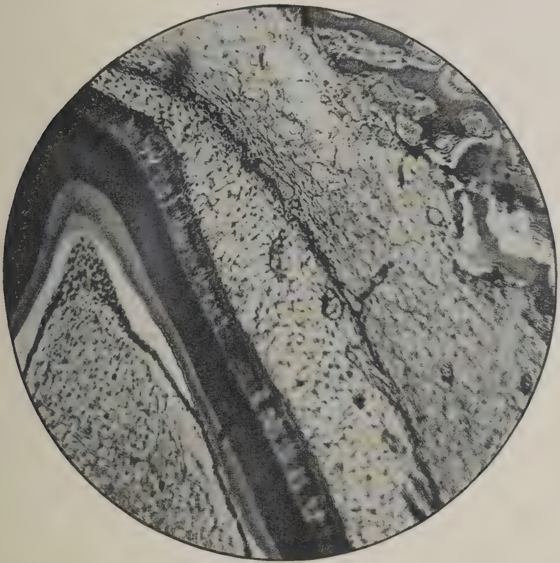

FIG. 104.—Showing the presence of blood vessels within the stellate reticulum of an enamel-organ of *Macropus billardieri*. (After Tims and Hopewell-Smith. Proc. Zoolog. Soc. Lond., 1911.)

Dr. Paul has adduced strong evidence in favour of Waldeyer's view, which has already been quoted in relation to Nasmyth's membrane.

So simple a matter as the vascularity or non-vascularity of the enamel-organ is not yet settled : Wedl asserts that it contains no vessels, Magitot and Legros sharing this opinion ; Xavier Sudduth has uniformly failed to detect vessels in it, but Dr. Lionel Beale, on the other hand, states that a vascular network lies in the stratum intermedium, and this is confirmed by Professors Howes and Poulton (13) in the rat ; and Hopewell-Smith and Marett Tims in a joint paper (10) have described the presence of vessels, containing blood corpuscles, in the enamel-organ of the wallaby (see

Fig. 104). [Bolk has also noted their existence in the enamel-organ of *Phascolarctus cinereus.* On the other hand, Martin has failed to discover them in *Dasypus novem-cinctus.*]

Paul, however, has uniformly failed to discover vessels in it, and is inclined to believe that those observers who have thought that they have detected them have been deceived by the very close resemblance to the stellate tissue of the enamel which is borne by the tissues external to the tooth-sac, which, after the disappearance of the stellate reticulum and the coalescence of the external and internal epithelium, would come to lie close against the enamel cells, bringing with them their rich supply of vessels. Leon Williams believes that in some animals the stratum intermedium itself becomes transformed into papilliform elements which contain vessels, and claims that in this respect the enamel-organ is vascular, and that his untouched photographs prove this. On the other hand, he states that this does not occur at the outset of enamel formation, and, apart from the inherent improbability of a change of an important kind in the formative organs without any corresponding change in the resultant tissue, the author cannot see that the photographs exclude Dr. Paul's explanation, as the stellate tissue seems always to have disappeared prior to the existence of these papillæ.

For his own part, the author has had under observation a very large number of enamel-organs, and he has never seen a blood vessel which appeared to him to be unquestionably in the enamel-organ. At all events, the origin of blood vessels in the tissue in the ordinary way of blood vessel formation is not likely to happen in a purely epithelial mass: if they do not originate in it, then, if there at all, they must have grown into it from without, *i.e.*, from the tooth-sac.

But none of those who claim that they exist have either described or figured their origin in either of these methods. Hopewell-Smith, who believes in the vascularity of the enamel-organ, has a photomicrograph in his "Histology and Patho-histology of the Teeth and Associated Parts," which is apparently quite inconclusive.

The inner surface of the enamel-organ, where it is applied to the dentine bulb, presents a perfectly smooth outline, but its outer surface is thus, at all events, in some animals indented by numerous papillary projections, into which enter blood vessels of the dental sacculus. It is believed that they exercise an influence on the formation of the enamel, to which again reference will be made; but their existence is denied by Sudduth during the period of activity of the organ.

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CHAPTER VI.

CALCIFICATION OF ENAMEL, DENTINE AND CEMENTUM.

Before proceeding to an account of the actual formation of the enamel it will be useful to discuss the question of calcification in general. A tissue is said to be "calcified" when the organic structures of which it is composed are hardened and stiffened by impregnation with salts of calcium. The impregnation with calcium salts may go on so far, that the residual organic matrix is reduced to a very small proportion, as is exemplified in the case of adult enamel, in which the organic constituents make a very minute percentage of the whole, so that practically the enamel wholly disappears under the influence of an acid; or the organic matrix may persist in sufficient quantity to retain its structural characteristics after the removal by solution in an acid of its salts, as is the case with dentine, bone, and cementum. There are two ways in which a calcified structure may be built up: the one by the deposition of the salts in the very substance of a formative organ, which thus becomes actually converted into the calcified structure; the other by a formative organ shedding out from its surface both the organic and inorganic constituents, and thus, so to speak, excreting the resultant tissue.

An example of the latter method is to be found in the shells of many molluscs, in which the mantle secretes the shell, and is able to repair fractures in it, without itself undergoing any apparent alteration; while the formation of dentine, bone, and enamel * are examples of calcification by conversion.

The insoluble salts of lime are altered in their behaviour by association with organic compounds, a fact which was first pointed out by Rainey (10), and has been more recently worked out by Harting (5) and Ord.

If a solution of a soluble salt of lime be slowly mixed with another solution capable of precipitating the calcium, the resultant lime salt will go down in the form of an amorphous powder, or, under some circumstances, in minute crystals. But in the presence of gelatine, albumen, and many other organic compounds, the form and physical character of the calcium salts are materially altered, and in the place of an amorphous powder there are found various curious but definite forms, quite unlike the character of crystals produced without the intervention of the organic substance.

Rainey found that if calcium carbonate be slowly formed in a

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* All observers are by no means agreed as to the details of the formation of the enamel. (Cf. p. 164.)

thick solution of mucilage or albumen the resultant salt is in the form of globules, concentrically laminated in structure, so that they may be likened to tiny onions. These globules, when in contact, become agglomerated into a single laminated mass, appearing as if the laminæ in immediate apposition blended with one another. Globular masses, at one time of mulberry-like form, lose the individuality of their constituent smaller globules, and become smoothed down into a single mass. Rainey suggests as an explanation of the laminated structure that the smaller masses have accumulated in concentric layers which have subsequently coalesced; and in the substitution of the globular for the amorphous or crystalline form in the salt of calcium when in contact with various organic substances he claimed to find the clue for the explanation of the development of shells, teeth, and bone. At this point Professor Harting took up the investigation, and found that other salts of calcium would behave in a similar manner, and that by modifying the condition of the experiment very various forms * might be produced. But the most important addition to our knowledge made by Professor Harting lay in the very peculiar constitution of the "calcospherites," by which name he designated the globular forms seen and described by Rainey. That these are built up of concentric laminæ like an onion has already been mentioned, and Rainey was aware that albumen actually entered into the composition of the globule, since it retained its form even after the application of acid.

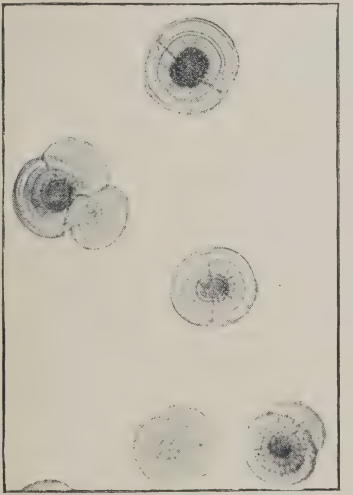

FIG. 105.—Calcospherites.

But calcoglobulin was also found in a comparatively amorphous

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* Thus he was successful in artificially producing "dumb-bell" crystals.

condition, formed without any precipitate round a crystal of calcium chloride plunged into albumen ; and it was further found that the presence of phosphates modified the result.

A precipitate obtained in gelatine and consisting of carbonate alone was at first membranous, but passed rapidly into the globular and crystalline forms : a precipitate of phosphate alone was at once crystalline without passing through any colloidal stage*, but a precipitate of bicarbonates and phosphates retained for an indefinite time this intermediate form ; and it is noteworthy that in bone, dentine and enamel phosphates and carbonates are invariably associated. Harting failed to produce calcospherites when experimenting with coagulated albumen, with tendons, or with decalcified bone matrix, but he succeeded with cartilage.

But Harting has shown that the albumen left behind after the treatment of a calcospherite with acid is no longer ordinary albumen : it is profoundly modified, and has become exceedingly resistant to the action of acids, alkalies, and boiling water, and, in fact, resembles chitin, the substance of which the hard integuments of insects consist.

For this modified albumen he proposes the name of "calcoglobulin," as it appears that the calcium is held in some sort of chemical combination, for its last traces are very obstinately retained when "calcoglobulin" is submitted to the action of acids.

The "calcospherite," then, has a true matrix of calcoglobulin, which is capable of retaining its form and structure after the removal of the great bulk of the lime, and this stains strongly with carmine and other stains.

Now it is a very suggestive fact that in the investigation of calcification structures remarkable for their indestructibility are constantly met with ; for example, if dentine is destroyed by the action of very strong acids, or by variously contrived processes of decalcification, putrefaction, &c., there remains behind a tangled mass of tubes, the "dental sheaths" of Neumann, which are really the immediate walls of the dentinal tubes.

Or if bone be disintegrated by certain methods there are separated large tubes, found to be the linings of the Haversian canals (Kölliker), and small rounded bodies recognisable as isolated lacunæ. The translucent pellicle of Nasmyth's membrane affords also another excellent example of this peculiarly indestructible tissue.

In point of fact, as will be better seen after the development of the dental tissues has been more fully described, there exists very constantly, on the borderland of calcification, between the completed fully calcified tissue and the formative matrix as yet not fully impregnated with calcium compounds, a stratum of tissue which in its physical and chemical properties very much resembles "calcoglobulin."

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* The subject of the behaviour of bio-colloids under varying conditions has attracted much attention in recent years. An interesting and suggestive paper is one dealing with the formation of agates, naturally coloured, from silicic acid jellies :—"Banded Structures ; Synthesis of Striated Stones," by Shanti Swarupa Bhatnagar and Krishna Kumar Mathur, in *Kolloid Zeitschrift*, Bd. xxx., 1922, pp. 368—371.—Ed.

It should also be noted that globular spherical forms are very frequently to be seen in the enamel cells, at the edges of the thin cap of forming dentine, and around the interglobular spaces (see Fig. 58); moreover, isolated spherules of lime salts have been described by Robin and Magitot as occurring abundantly in the young pulps of human teeth, as well as those in the Herbivora, where their presence was noted by Henle. Perhaps all deposit of calcium salts commences in this way.

In an instructive paper, the late Sims Woodhead (16) advocated the view that a calcification is in some measure a change in the direction of degeneration, for which there are needed (1) devitalised tissue in which albuminoid matter is present; (2) a layer of formed material such as fibrous tissue or some membrane (in bone both of these are represented by the matrix, the fibrous tissue of which, in the centre of one of the trabeculæ, is practically devoid of cells, the layer near the surface being merely a membrane in which a few cells remain); (3) the layer of proliferating cells always found in the region of any foreign or dead mass, these cells being the osteoblasts of bony tissues, and amongst their functions, as regards calcification, perhaps the most important being the generation of carbonic acid.

He writes: "The osteoblasts lay down a matrix of formed material; the more active the cells within certain limits the greater the relative amount of the matrix. This matrix may be looked upon as inert or dead organic matter, which corresponds to a membrane through which dialysis may take place, or rather the layers near the two surfaces may be so considered, and as the molecular combinations of the phosphoric acid and lime take place around the osteoblasts (which, as before stated, during their active formative stages give off carbonic acid to render the lime for the time being insoluble), there is a continuous process by dialysis of separation of these lime salts. We look upon the formed dialysing membrane that serves to separate the lime salts prepared in its immediate neighbourhood by the carbonic acid forming cells; this carbonic acid causes a throwing down of phosphates of lime, with a small proportion of lime in which the phosphoric acid is usually replaced by carbonic acid."

If Hoppe Seyler is correct in supposing that the salt which hardens bone, dentine, and enamel is a double salt, in which one equivalent of lime carbonate is combined with three equivalents of lime phosphate, then the share taken by the carbonic acid set free under Sims Woodhead's theory becomes easily understood. (Cf. p. 41.)

It must be remembered, however, that in all these experiments carbonates give the best results without phosphates, and the experiments must be regarded as a parallel to, rather than as actually reproducing, what goes on in actual calcification.

Calcification of the Enamel.—Although the calcification of the dentine commences before that of the enamel, it will be convenient to describe that of the enamel first, as being perhaps a somewhat simpler and more easily intelligible process.

Two views have been held as to the formation of this tissue, (i.) that it is formed by the actual conversion of the cells of the enamel-organ into enamel ; (ii.) that it is in some sense secreted or shed out by these cells. In support of this latter theory the names of no less authorities than Huxley, Kölliker, Magitot, and others may be adduced, but some of the grounds on which their decisions were based are appearances susceptible of a different interpretation. Kölliker considers that the cells do not undergo any direct conversion, but that the enamel is shed out from the ends of the enamel cells, the enamel fibres therefore corresponding in size and being continuous with the enamel cells whence they were shed out.

The cells would thus elaborate, and, so to speak, plaster from their free ends the material in question upon the already-formed enamel, they themselves retaining their own integrity. Without laying too much stress upon an analogy which is only partial, there may be cited the resemblance in the resultant products in the case of enamel, and in the case of the shells of certain molluscs, say, for example, *Pinna*. In the latter the shell is formed intermittently by the margins of the mantle, which are closely applied to it, but are at any time separable, so that it is difficult to suppose that any conversion of its constituent cells can take place. It would rather seem certain that something must be shed out from their ends, which is hardened by the deposition in or with it of calcium salts. The shell of *Pinna* contains so large an amount of organic matter that its structure is retained even after the removal of the lime by means of an acid ; and it is conceivable that the cells of the mantle are at work, elaborating their products like so many bees plastering wax upon a honeycomb.

But whether the enamel cells manufacture something which they shed off their extremities, or are themselves converted into hard tissue by the deposition of calcium within their own substance, no one doubts that they preside over the process and determine the form of the result.

The cells of the internal epithelium of the enamel-organ or enamel cells have been already in some measure described. They are elongated cells, forming a very regular columnar epithelium, and are hence rendered more or less hexagonal by mutual apposition. [According to Carter([4a]) the ameloblasts of the marsupial enamel-organ at an early stage are not in apposition laterally, but are separated by a homogeneous acidophile intercellular matrix. At a later stage the ameloblasts seem to be again separated from one another by intercellular areas which are now crossed by cell-bridges.] The ameloblasts vary in their length and diameter in different animals, but always correspond in diameter with the complete enamel rods.

To secure uniformity of nomenclature, the name ameloblast has been proposed for them, as being better comparable with the terms odontoblast and osteoblast.

Although they are connected with the cells of the *stratum intermedium* by a process at their bases, they often adhere more strongly to the enamel, when once this has begun to be formed, than to the rest of the enamel-organ, so that when a dental capsule is opened the enamel cells are most easily obtained by scraping the surface of the enamel. The cells thus torn away often have tapering processes at the ends directed towards the enamel, and are called "Tomes' processes." The cells are also slightly enlarged at these extremities, especially if they have been immersed in glycerine or any such fluid which causes their shrinkage, perhaps because this end of the cell having received a partial impregnation with calcium salt at its periphery, and therefore being rigid, is unable to contract with the rest of the cell. These enlarged, everted ends often show a very sharp contour, their trumpet-like mouths tending to confirm the statement of Waldeyer, that the protoplasm of the cell is not covered by membrane at its ends. The nucleus is large and oval, often occupying the whole width of the cell, and it lies near to that end of the cell which is farthest from the forming enamel. It contains granules of chromatin, and is of delicate reticular structure; there are also generally one or several nucleoli.

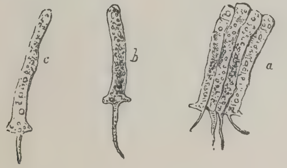

Fig. 106.—Enamel cells with Tomes' processes.

Sometimes the nucleus is square or angular. It is not uncommon for it to appear crescentic on section, the horns of the crescent being directed towards the young enamel (Fig. 111), and there is also sometimes an appearance as though the horns were continued into filamentous processes. If such processes have any real existence, it is very possible that these shapes of the nucleus may be due to its being, so to speak, dragged upon during its recession from the forming enamel; for there is practically no doubt that a single ameloblast forms the whole length of an enamel rod, and therefore is constantly receding as more enamel is formed. There is also a delicate reticular appearance in the body of the cell, and, in addition, there are to be seen little spherules or oval bodies, transparent, structureless and highly refractive, which sometimes attain to considerable size. These were first described by von Spee, and afterwards by Andrews, who believed that they represent the formative material of enamel, and attached therefore much importance to them.

They stain black with osmic acid, as does also the youngest layer of forming enamel (Röse), and it has been pointed out by Leon Williams that, in double-stained sections, they often take the same colours as the contents of the blood-vessel, whence he concludes that they have some albuminous constituent. [Carter,* however, regards them as alveolar spaces, the walls of which are basophile and their contents acidophile.] Ameloblasts vary much in length. They are longest when enamel formation is most active, and a material thickness of enamel is to be formed. Their distribution coincides always with the extent to which functional enamel is going to be developed upon the tooth, as is observed in the development of the teeth of fishes. As has been already mentioned, the ameloblasts in some parts of the enamel-organs of certain fish, such as the eel and perch, and certain *Batrachia*, *e.g.*, the newt, have dimensions very greatly exceeding those of the cells in the remainder of the organ. These highly

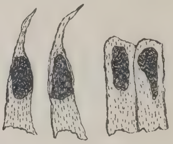

FIG. 107.—Enamel cells; the two on the left have been shrunk by immersion in glycerine and present the open trumpet-shaped ends described in the text.

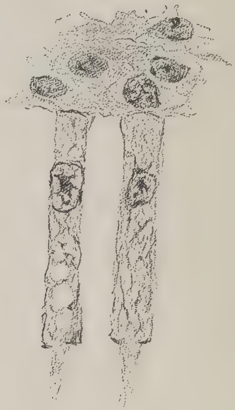

FIG. 108.—Enamel cells, showing the apparently reticular structure of the plasm of the cell, the globular bodies (in the left-hand cell), and the Tomes' processes. At the top of the figure is a portion of the *stratum intermedium*. × 1,000.

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* Mr. Thornton Carter's paper gives a detailed account of the changes which occur in the ameloblasts and their nuclei during enamel formation in the marsupials (4a).—ED.

developed bodies, three times as long as the corresponding ones lower down upon the dentine papilla, are in the position of the terminal cap of enamel which characterises the teeth (Fig. 99). Moreover, in the tooth sac of the poison fang of a viper, the distribution of the large cells coincides with that of the enamel on the finished tooth (Fig. 109).

Notwithstanding all that has been written upon the subject of enamel development, the problem is so difficult that some doubt still remains as to the exact *modus operandi* of the enamel cells, though no one now doubts that they are the active agents in the process, and their diameter corresponds exactly to that of the completed enamel rod in the particular animal.

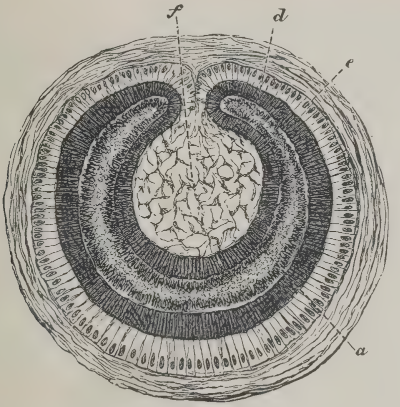

FIG. 109.—Transverse section of the tooth-sac of a poison fang (viper). The crescentic pulp (*a*) is surrounded by a layer of dentine (*d*). External to this is a layer of columnar ameloblasts, which, upon the exterior of the tooth, in the situation where a thin layer of enamel is to be formed, are large conspicuous cells. As they pass in between the horns of the crescent, into that part which will ultimately be the poison canal, their character is lost, and their places taken by the stellate cells (*f*). No enamel is formed in this latter position.

Tomes' processes are of universal occurrence in all mammals which have been examined, and there is no doubt that they enter the youngest layer of enamel. And it has long been known that from the surface of growing enamel acids can detach a fenestrated membrane, as though, at this stage at all events, the cementing material were a little more resistant than the axes of the rods, and it has been inferred that Tomes' processes had been pulled out of the holes thus demonstrated. [This structure Carter regards as being formed by a modification of the protoplasm of the inner expanded ends of the ameloblasts and not a membrane in the true sense, but nevertheless it functions as a dialysing membrane.]

Many years ago it was pointed out that Tomes' processes were of nusual length in marsupials, and that this might have some bearing upon the question of enamel development. [On the other hand, Carter believes that Tomes' processes are not cytoplasmic prolongations of the ameloblasts, but are the result of ameloblastic secretion and are purely metaplasmic products (4a).] It is probable that in marsupial enamels lies the clue to enamel development in general (12b).

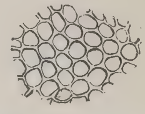

FIG. 110.—Fenestrated membrane raised from the surface of forming enamel by dilute hydrochloric acid.

Andrews (2) had pointed out that a fine fibrillar structure is to be seen near growing enamel between the ameloblasts and the enamel, and these fibres have been seen and figured also by Leon Williams; but neither of these observers has appreciated their full importance, owing to their having only investigated enamels in which their existence is very transitory. But in the tubular enamel of marsupials they persist and can be seen extending the whole distance between the ameloblasts and the layer of young dentine, and can

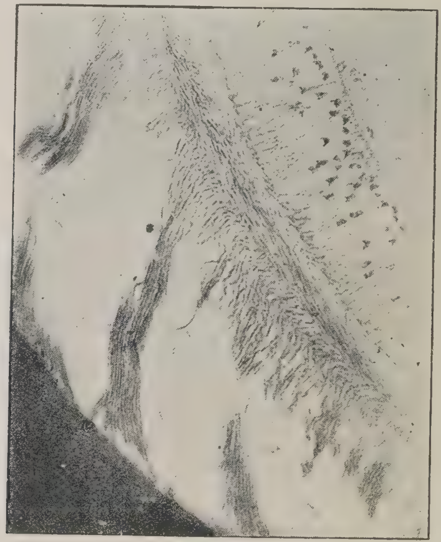

FIG. 111.—From a developing tooth of *Macropus*. At the right-hand top corner is the *stratum intermedium*, next the ameloblasts, with somewhat angular nuclei; and from these soft fibrils extend in places right across to the dentine, which is the dark mass at left bottom corner of the figure. A short distance from the ends of the ameloblasts the fibrils are seen to change their direction abruptly.

hence be studied to far greater advantage. They are there clearly seen to be merely very long Tomes' processes (which are in fact fibrils broken off short), and it is obvious that they are the prolongations of the plasm of the ameloblasts, which, as rightly described by Waldeyer (13), have no membrane across their free ends; their behaviour to stains is the same as that of the cell contents. Although it is convenient to speak of them as fibrils, they do not show any minute fibrillar structure. Where they leave the parent cells they are apparently not much, if at all, smaller than these, the small size of Tomes' processes in human enamel being perhaps due to their having been attenuated by being pulled from the enamel. They are soft and extensile, so that they may be drawn down to a mere thread before they break (see Fig. 112), and their direction exactly coincides with that of completed enamel rods, running straight where these do so, and taking abrupt bends when these bend, as they often do, almost at right angles in certain parts of the kangaroo's enamel.

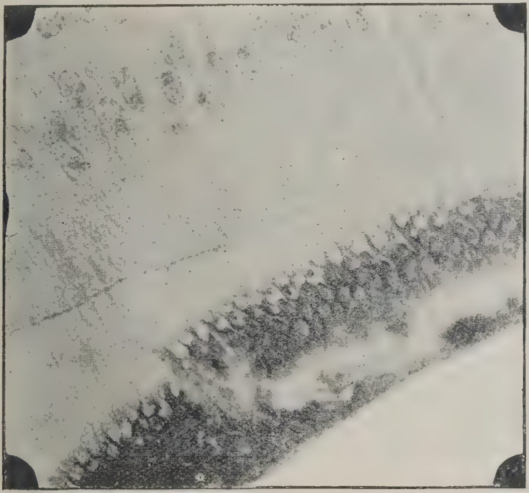

FIG. 112.—Ameloblasts, Tomes' processes, and youngest part of enamel of *Halmaturus*, which is cut slightly obliquely, and has the appearance of a honeycomb. The Tomes' processes are drawn out thin by the slight displacement of the ameloblasts, especially at the left of the figure, and their continuations may in places be seen in the openings of the honeycomb. × 1,000.

In decalcified sections of developing marsupial enamel, if, as generally happens, they are in the least degree oblique to the axes of the rods, there is a most conspicuous appearance of a sort of honeycomb, the septa of which take stains strongly. The Tomes' processes, and their continuations the fibrils, enter the spaces of this honeycomb, and in favourable sections which happen to be transverse to the honeycomb are seen to fill the holes. [According to

Mummery these processes divide into bundles which interlace in the honeycomb region and furnish the major portion of the fine fibrillar matrix of the enamel ([8b]).] This conspicuous honeycomb is exactly the same thing as the fenestrated membrane already alluded to (p. 168) in human and other mammalian enamels, but in enamels which are to have solid rods it occupies only a very small vertical depth, while in tubular enamels it is of material thickness. In addition to marsupials, it can be seen in the pig and the sheep, quite recognisable as a honeycomb, and it is distinctly visible in some of Leon Williams' photographs. But although it is comparatively thick in marsupials, yet it is in them, like the fenestrated membrane of older observers, a transitional structure belonging to one—the earliest—stage of enamel calcification, and when a little farther advanced towards completion it loses its resistant power and becomes dissolved by the decalcifying agent. Hence in decalcified sections the fibres are seen at first, close to the ameloblasts, free; then attached together by the honeycomb; while deeper in the forming enamel they are more or less free again.

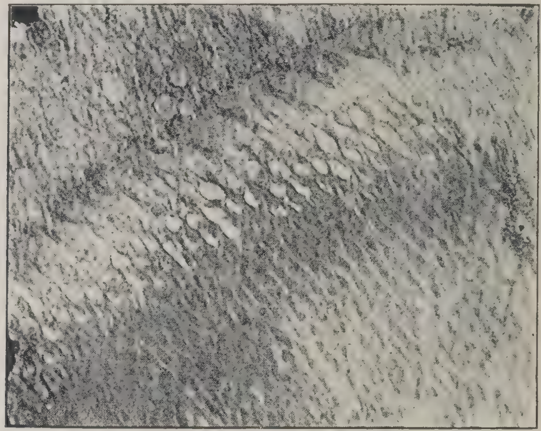

FIG. 113.—The ameloblasts of *Halmaturus*, cut so obliquely as to be hardly recognisable in the figure, lie to the left upper side of the figure; next comes the honeycomb region; while the lower part of the figure is occupied by more developed enamel, in which the fibrils may be seen, cut obliquely, as darker masses. Thus in the earliest honeycomb stage the septa stain more strongly than their contents, but at a later stage the fibrils stain more deeply than the septa. × 1,000.

The exact relationship of the fibrils to the cells of the honeycomb was at first difficult to understand, for while in cross section they are seen to occupy the lumen of each cell, and could be in this position in longitudinal section also, yet, especially when drawn out so as to become attenuated, they seem to be adherent to the septa. Moreover, the septa of the honeycomb are thicker than the amount of interstitial substance found between the rods in complete enamel would account for. But it was found that although their external portions ran continuously into the substance of the septa, their internal portions were still soft, so that the fibril slightly pulled upon, in cutting the section, took on a sort of hour-glass shape, its ends attached to the ameloblasts and to the septa of the honeycomb remaining of their original diameter, while the intervening portion was drawn out into a thread. Hence it appears that the first changes in the fibril towards calcification take place in its exterior, and progress towards its interior, which in the case of marsupial tubular enamel they may never reach, many of the rods continuing to have a canal with soft contents down its axis. But in enamels with solid rods the full calcification of the whole thickness of the fibril follows very closely upon the heels of the first honeycomb change, and so the nature of the process is masked.

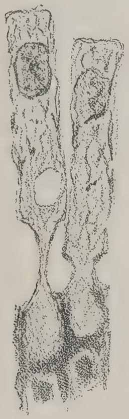

Fig. 114.—Ameloblasts of *Halmaturus* showing their relation to Tomes' processes and to the honeycomb; the latter is cut slightly obliquely, so that, below, a second cell is opened into.

It is probable, therefore, that the ameloblast itself does not calcify;

That each ameloblast furnishes a fibrillar process, continuous with its own plasma, which serves for the entire length of an enamel rod;

That calcification and the changes preparatory to calcification take place in or round each fibril, quickly reaching its central axis in solid enamels, but never reaching it in some of the rods of tubular enamels.

It will be seen that the appearances are consistent either with the calcification of the fibril, or with calcification going on round it, and, so to speak, reducing it down to smaller dimensions or obliterating it.

The exceedingly small amount of organic matter present in completed solid enamel might seem to point to the latter being the preferable view, but were this so, one might have expected the individuality of the rods to be lost, whereas there appears to be an appreciable amount of interstitial substance demonstrable between them.

It has been pointed out by Leon Williams that the axis of the ameloblasts seldom coincides with that of the rods ; this is the case, the ameloblasts always standing nearly at right angles to the dentine surface. But though these fibrillar prolongations start off in the same direction as the axis of the cell, they, in many cases, change their direction quite abruptly a little way from the cell, and the directions which they then assumed correspond exactly with those of the rods in the completed enamel. The identity of the fibrils with the ultimate canals of marsupial enamel is further shown by the former, in the more advanced parts of the enamel, being spiral.

If this theory of enamel formation be correct, it serves to explain much that was heretofore perplexing. In the first place, in marsupials the extent to which the tube system exists varies much in different members of the group, and even in those in which it is most rich the tubes become smaller as they approach the outer surface and disappear well before they reach it ; so that it is quite obvious that the same enamel-organ is capable of forming both tubular and solid enamel, and there can hardly be any very fundamental difference in the processes.*

In examining a marsupial enamel-organ no dissimilarity can be seen between the different ameloblasts—every one has its long Tomes' process. Yet in the finished enamel the majority of the rods are solid, as may be seen in Leon Williams' beautiful photographs of transverse sections of kangaroo enamel. Whilst taken over a considerable area, the tubes seem somewhat evenly distributed, though sometimes two or even three contiguous rods contain tubes, similarly four or five contiguous solid rods may easily be found. On the whole a tube occurs in about one out of every four rods in the kangaroo.

Again, the enamel-organ of a marsupial, prior to the formation of any enamel, is absolutely indistinguishable from that of another mammal ; and tubular enamel reappears sporadically amongst other very diverse mammals, for instance in the *Hyrax*, in certain *Insectivora*, and in the *Jerboa* among rodents.

But if tubularity is a stage through which every enamel rod passes, the difficulty of accounting for animals, whose allies have all lost it, reacquiring or developing it, disappears. And although the examination of human or other solid developing enamels might never have led to this interpretation, yet a re-examination of them, after having arrived at it, convinces the observer that it is equally true of all.

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* Mr. Thornton Carter exhibited sections of enamel in a large number and variety of mammals at a recent scientific meeting of the Zoological Society of London. It was proved that tubular enamel is of much wider occurrence than had previously been supposed. Mr. Carter's paper is as yet unpublished. It will be awaited with great interest, as it will be evident from the above that it should prove of very considerable importance in the elucidation of this most difficult problem of enamel calcification.—Ed.

Andrews unquestionably had the fibrils of the ameloblasts under observation, and was probably the first to describe them. But he described them as coming from the cells of the *stratum intermedium*, which they certainly do not; and he speaks of them as a fibre network, which, when the enamel rod is fully calcified, is wholly obscured; and neither he nor Leon Williams appreciated the importance of their *role* nor their relations to the rod; indeed, it is to be doubted if it were discoverable elsewhere than in a tubular enamel. The latter observer noticed the complexity of the course of the fibres which he saw, but apparently did not connect it with the complexity of the course of the enamel rods in the animals from which his sections came. But in a much earlier paper (1) he came very near to the above views when he wrote: "As the formation of the enamel progresses, these cells recede, leaving within the formed enamel what appears to be a fibre of living matter in the centre of the enamel prism."

Röse's views nearly coincide with these, and he correctly figures the appearances so far as they are visible in human enamel. He, however, takes a somewhat different view of the process; he describes the young enamel as like a honeycomb with Tomes' processes in the cells of the honeycomb. He considers that young enamel, like young dentine, has an organic matrix fairly rich in calcium salts, but as yet not by any means fully calcified, and that the lime salts are first deposited fully in the Tomes' processes, so that at a certain stage young enamel consists of thin rods (calcification in Tomes' processes) with a large amount of interprismatic substance; the rods then thicken, so that finally there is but a mere trace of cement substance between them.

Von Spee and Andrews consider that the globular bodies described by them in the ameloblasts, and particularly near their free ends, coalesce and merge into the enamel substance, the fibres they describe perhaps serving as a sort of scaffolding to determine their arrangement. This again is not far from the true nature of the process, and this idea is adopted, with modifications, by Leon Williams (14), who, in his later paper, holds that these globular bodies pass out from the ameloblasts, and are seen to be connected with one another by plasm strings, several to each rod, which strings can be seen in the body of the ameloblast, where they constitute the reticulum above described. He holds that in the formed enamel rod these globular bodies are more or less compressed into disk-like shapes, and are sometimes nearly, or quite, melted into one another. This is in effect a close approach to the older view of Harting, who writes: "Les prismes, qui composent l'émail des mammifères, ne sont évidemment que des piles de calcospherites très petites," &c.

Leon Williams further says: "Around the skeleton thus formed, which constitutes the real structure of enamel, the albumen-like substance flows, supplying the cement substance, and probably the mineral matter for the whole."

This view differs from that propounded in the text, in that it does not recognise the preponderant importance of the ameloblast processes and in that it puts first the formation of the rods, to be afterwards joined together by a cement substance, whereas it is probably beyond dispute that the first thing formed is the periphery of the rod and the uniting cement substance, for in the honeycomb the septa of contiguous cells are already united and appear homogeneous, which is a sequence of events quite different from that which he indicates.

Kölliker, partly upon the ground that ameloblasts can be seen of the same size and form at all stages of enamel formation, held that enamel formation was one of secretion, the enamel being shed out, so to speak, from the free end of each enamel cell ; hence the rods of the enamel will correspond in size and number with the cells of the enamel epithelium. The processes of the ameloblasts he regards as being fragments of this hardened secretion which are still clinging to the parent cell.

Legros and Magitot (⁶) revived this view, describing each cell as terminated, towards the forming enamel, by a little plate of dense material through which by some process of osmosis the constituents of enamel travel out. They note that these plates often cohere so as to form a sheet, but say nothing of their being perforated. No one, however, who had seen the enamel cell of a marsupial with the tapering process five or six times as long as itself which had been pulled out of the young enamel would be satisfied with the excretion theory as so expressed.

Schwann believed that the enamel cell was constantly increasing at its free end (*i.e.*, that next to the enamel), and that the new growth, or youngest part of the cell, is calcified as fast as it is formed. This view differs little from that of Kölliker, who prefers to express it by saying that this end of the cell is constantly shedding off or secreting a material which becomes external to itself. Sir John Tomes, Waldeyer, Hertz, and many others, believed that the cell growth takes place not at this free end, but at the attached nucleated end, and that it is the oldest portion of the cell itself which receives an impregnation with salts and forms the enamel.

[Mummery and von Ebner do not endorse the views put forward by the author, the fundamental difference being that the latter regards the tubes of the marsupial enamel as being entirely an enamel formation, and the process of calcification as being centripetal and incomplete, leaving the processes uncalcified in the centre, while in other mammals it is complete, whereas the former writers consider the tubes to be dentinal processes included in the enamel and that calcification is due to a regular deposit of calcified granules in the fibrils of the honeycomb layer with which Tomes' processes are incorporated. The process of calcification is therefore interprismatic and centrifugal.

Carter's view may be given in his own words (⁴ᵃ, p. 298): "Enamel is regarded as the product of changes similar to those passed through by other colloidal media in solidification, *i.e.*, a continuous phase, organic in nature and of a honeycomb structure, being produced by gel formation, in the cavities of which lies a dispersed phase rich in calcium, but poor in organic material. The enamel appears to calcify from adsorption of the calcium into the organic matrix, and this proceeds, until eventually the cavities of the honeycomb are completely filled and obliterated, when the pattern of the fully formed tissue can be made evident only by the use of a decalcifying agent, which acts unequally on the rods and on the interprismatic material."]

Upon the question of the nature of the globular appearances and smaller beads observed in the ameloblasts, any positive opinion must be still reserved. It may be that von Spee, Andrews, and Williams are right in believing it to be material elaborated for the purpose of calcification, and they may be right in supposing that these masses migrate bodily from the ends of the cells. The evidence does not seem, however, to be conclusive.

Leon Williams describes appearances which lead him to believe that there is a membrane at both ends of the ameloblast, because in some double-stained preparations there is a sharply defined line of a different colour, both between the enamel and the dentine at the earliest period of calcification, and at all periods between the ameloblasts and the stratum intermedium. But differences in staining occur frequently in the very same tissue, and merely indicate a slight difference in state, and it is perfectly certain that there is no membrane over the free end of the ameloblast after the formation of its fibrillar prolongation ; whilst in intervals between two fibrils there is often a very defined line, which, if the section does not happen to lie exactly along the central axis of the cell, looks to be continuous over many cells and their processes, so that the appearances are open to a different interpretation. He himself is aware that later on there is no membrane and can be no membrane ; and appearances of membranes seen in section are open to so many fallacies that, where there is an *à priori* improbability in the existence of one in a particular position, it is safer to doubt its existence until it is demonstrated more extensively.

With regard to the other constituents of the enamel-organ there is not very much to be said. Behind the ameloblasts come the large round cells of the *stratum intermedium.* It has been customary to attribute to these the function of recruiting the enamel cells, with which some observers have believed them to be connected by processes. After the disappearance of the stellate reticulum, the tooth-sac, rich in blood vessels, closely applies itself to the *stratum intermedium ;* and hence may have arisen the supposition that the enamel organ contains blood vessels, the strong resemblance of the structures just outside the stellate reticulum lending itself to this mistake. Since, then, this layer is made up of large cells and intervenes between the ameloblasts and their blood supply, it is highly probable that it takes some active share in the elaboration of the materials required for enamel formation, but what that share is is unknown. The inner surface of the tooth-sac is frequently produced inwards into papilliform eminences, to which some observers have even attributed the function of planning the pattern of the enamel rod, and when it has come down upon the *stratum intermedium,* these are said in some cases to become even more conspicuous.

Leon Williams, seeing this large development of the cells of the *stratum intermedium* distributed over vascular papilliform shapes, has attributed to the cells a glandular function, and sets down to them a very large share in enamel formation in the way of elaborating products for calcification. But this is hardly a safe inference. In the first place, this particular structure does not arise till after some enamel is already formed, and there is no known difference between the enamel formed before and after its development ; moreover, it is only in some animals that it is at all well marked, and their enamel is not different in any known way from those that do not possess it.

[Carter states (^{4a}) that at a later stage of enamel formation in marsupial teeth the cells of the *stratum intermedium* can often be seen insinuating themselves between the ameloblasts and functioning as such. At this stage the ameloblasts appear to be rejuvenated, and coincidently some of the cells of the *stratum intermedium* degenerate, and Carter suggests that the products of degeneration may pass over the intercellular bridges and supply a pabulum for the regeneration of the ameloblasts. On the other hand, Mummery states (8c) that any recuperating effects which the cells of the *stratum intermedium* may have on the ameloblasts can only occur by osmosis owing to the presence of the " outer ameloblast membrane " between the two layers of cells. Carter, however, denies the existence of definite ameloblastic membranes.]

The ultimate fate of the external epithelium was treated of when describing the minute anatomy of Nasmyth's membrane, so no more need be said here.

Upon the whole, then, it must be admitted that although advance has been made in recent years towards a clearer conception of the process, there still remains a great deal to clear up with regard to precise knowledge of enamel formation and even of the structure of enamel itself.

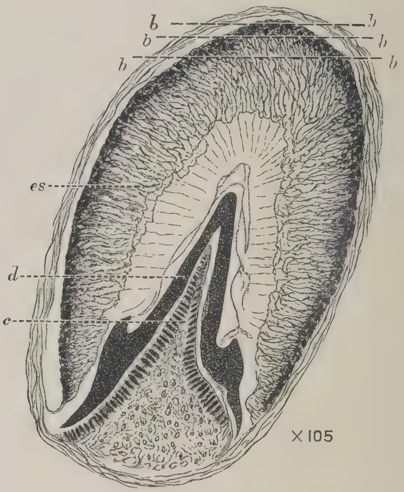

FIG. 115.—Tooth-germ of hake (*Merlucius*). *b*. Stained outer border of enamel stroma. *c*. Dentine-papilla. *d*. Formed dentine. *es*. Enamel stroma. The formed dentine has disappeared in decalcification, leaving merely traces of its former structure. (From " Roy. Soc. Lond. Phil. Trans.," B., 1900.)

The Calcification of the Enamel in Fish.—On this subject knowledge is somewhat fragmentary. The process has been investigated in a few osseous fish and in Selachians (11c and 11d).

It was hoped to find methods transitional between those peculiar to Selachians and those found in mammals when investigating osseous fish, but instead another quite peculiar process was found, the bearings of which on enamel development in general are a little difficult to decipher. In the *Gadidæ* small lance-like or spear-shaped caps of enamel surmount the apices of the teeth (see Fig. 69), the rest of the organs being apparently devoid of enamel, or perhaps having only a rudimentary layer. In an early stage the tooth-germ is just like a mammalian tooth-germ.

But very soon preparation is made for the enamel caps, which will ultimately remain in a groove at the apex of the dentine, so that they do not greatly increase the diameter of the tooth. At the period when the calcification of the dentine is about to commence, the ameloblasts, where the cap of enamel is to be, enlarge greatly, and there comes to be a considerable space in the tooth-sac (which is formed by a condensed connective tissue) above the dentine-papilla. Up to this point the ameloblasts, which are about 19μ in length, only differ from the mammalian type in that their nuclei are not quite so sharply marked, and the plasma stains somewhat more freely.

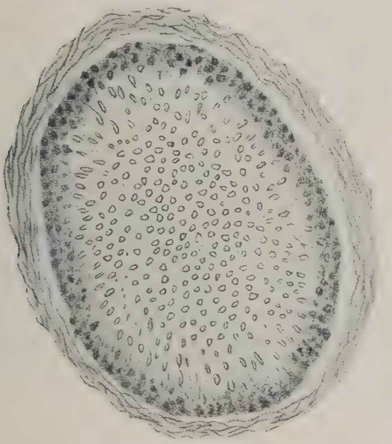

Fig. 116.—Transverse section of enamel stroma of hake, taken in the region indicated by the lowest dotted line marked *b* in the preceding figure. × 120. ("Roy. Soc. Lond. Phil. Trans.," B., 1900.)

When a thin shell of dentine has been calcified, the space above the dentine occupied by the ameloblasts has again greatly increased, and has attained to the full dimensions of the ultimate enamel cap; the ameloblasts have disappeared altogether, having become transformed into a tissue which in longitudinal section looks like a very delicate connective tissue with elongated meshes. Seen in transverse section, it is found to be perforated by holes arranged with the utmost regularity (Fig. 116).

No nuclei are to be found in this stroma, but round its outer surface are closely grouped nuclei which are the same size as, and may possibly actually be, the nuclei of the ameloblasts. Later on in transverse section the holes already alluded to have become smaller and are surrounded by thick borders which take a stain, but although the outer portions of these areas are not sharply defined, they have not actually coalesced with one another (Fig. 117).

Without entering into full details, which may be found in the paper referred to, the peculiarity of the process is that instead of the ameloblasts, as in mammalia, building enamel with a very small amount of transitional tissue between the cells and the fully formed enamel, these cells become bodily transformed into a stroma, which is of the full size of the enamel to be formed, disappearing themselves as individual sharply defined cells.

Blood vessels are very abundant in the connective tissue which forms the capsule, but none enter the enamel-organ.

Hence arises the anomaly of calcium salts being separated out and deposited in a stroma of considerable thickness without there being any conspicuous cells to effect its segregation, unless indeed the nuclei of the ameloblasts have persisted.

Apparently the enamel rods are at first tubular, for the centres of the bodies figured in Fig. 117 look empty: if they are solid columns the material of which they are composed will not take any stain.

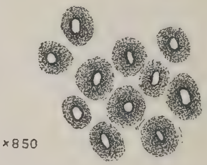

Fig. 117.—From the outer and darker peripheral portion of the section last figured. ("Roy. Soc. Lond. Phil. Trans.," B., 1900.)

The enamel when finished is at first sight structureless, but in fortunate sections a striation running in from the free surface, something like that seen in *Sargus* (see Fig. 45), can easily be traced.

The development of the enamel in *Sargus* and in the *Labridæ* has been worked out by Howard Mummery (8d). He finds in *Sargus* that the enamel is at first laid down by ameloblasts to form the dense layer which is not perforated by the outer system of enamel tubes (*vide* p. 68). After this has been laid down the ameloblasts and the cells of the external epithelium disappear, their place being taken by tubes and a delicate stroma. The future outer tubular portion of the enamel is seen to be occupied by vascular spaces continuous with the blood vessels of the capsule. Between these blood spaces are tube-like processes which at their deeper ends become merged in the stroma. In the latter are irregular-shaped bodies which Mummery regards as the calcoglobulin basis of the spherites. The intervascular tissue he regards as having a secreting function.

In the *Labridæ*, blood vessels also enter the enamel-organ and alternate regularly with a secreting organ, which is a true secreting structure and which in some members of the family assumes the form of a tubular gland, formed by a direct conversion of the enamel-organ (^{8d}).

[Carter (^{4b}) finds no sign of vascularity of the enamel-organ in the hake, though it is richly invested by capillaries. Though he had no opportunity of examining the genera which Mummery investigated, Carter examined *Pagellus centrodontus* and *Labrus bergylta*, and these, he says, lend no support to Mummery's view ; he finds ameloblasts persisting throughout enamel formation where Mummery finds glands and ducts.]

In the elasmobranch fishes the departure from the mammalian methods is still more extreme, and the tissue formed is sufficiently different to have been variously described as enamel and as vitrodentine (see p. 62).

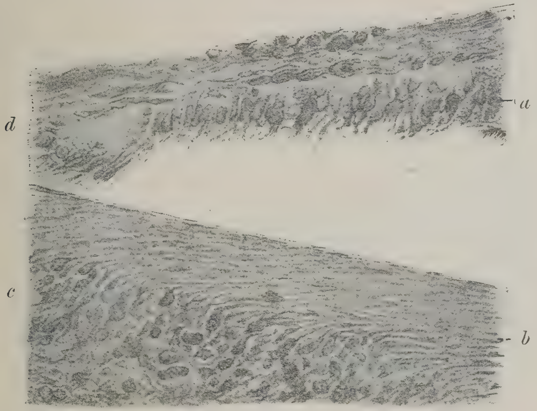

Fig. 118.—Portion of young tooth-germ of *Lamna*. × 240. *a*. Ameloblasts, not yet fully developed. *b*. Specialised surface layer of pulp. *c*. Dentine pulp.

An early tooth-germ does not differ much from an early mammalian tooth-germ : there is the cap of enamel-organ, and a dentine-papilla, the surface cells of which are not at all differentiated (cf. Fig. 120). But before any calcification has commenced the peripheral cells of the dentine-papilla have become spindle-shaped, with immensely long processes which become parallel with the surface, and finally constitute a very definite layer of considerable thickness.

When calcification commences it is not on the surface of the dentine-papilla, but a little way inside it, beneath the specialised layer just described. Hence this fibrillated layer is left between the cells of the enamel-organ and the first formed dentine, which latter speedily cuts it off more or less completely from the subjacent pulp, and it is noteworthy that this layer corresponds pretty closely in thickness with the future enamel.

So far no mention has been made of the enamel-organs, the change described having taken place entirely in the mesoblastic dentine-papilla. If a vertical section of the jaws of a Selachian be examined, the nature of the succession places before the observer, at a glance, a series of tooth-germs of all ages, the youngest being at the bottom (cf. Fig. 96). In this, *e.g.*, in *Lamna*, the ameloblasts are about 18μ in length ; over the next papilla they have increased slightly, while over the third in respect of age and position they suddenly extend to 65μ, 70μ, or even more, often being quite four times the length of the younger ones. Again, in the next tooth-germ above this, they have suddenly dropped to about 16μ, and at the same time have changed their appearance and their staining reactions completely. In the youngest ameloblasts the plasma stains pretty freely, even with nuclear dyes : in the largest cells it does not stain at all, and it is very transparent, while their nuclei stain deeply. Over the next older tooth the glassy appearance is gone, the plasma stains and the nuclei do not, so that they look like holes in the cell.

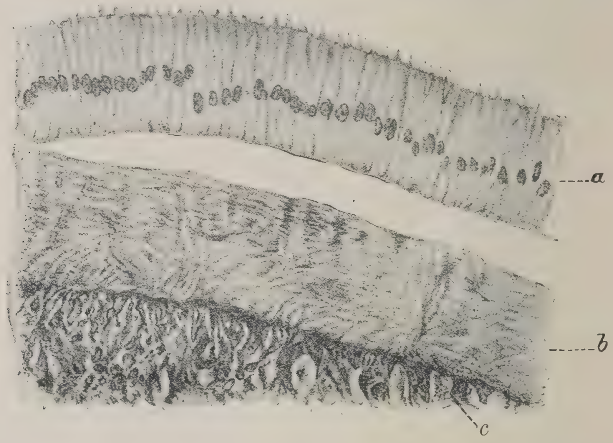

FIG. 119.—Tooth-germ of *Carcharias*, at an older stage than Fig. 118. × 200. *a*. Enormous ameloblasts. *b*. Specialised outer layer of dentine pulp. *c*. Body of dentine pulp with calcification commencing between it and the specialised layer.

Now this enormous development of the ameloblast cells coincides in point of time with the calcification of the outer fibrillated layer of the dentine-papilla, which is very rapidly accomplished. As soon as it is done they are obviously spent and degenerated, as seen by their shrinkage and the change in their nuclei. It is hardly possible, therefore, to doubt that they effect its calcification, especially when it is remembered that this layer has already been cut off from the subjacent dentine-papilla by the rim of calcification of dentine which has already been formed. Moreover, there is no other function for them to fulfil, as no other tissues are formed, and one cannot suppose that their sudden and enormous development is for no purpose.

The process, as described, is common to all of the elasmobranch fishes, but it varies in degree according to the tissues to be ultimately formed. Thus while the fibrillar layer is thick in *Lamna*, *Carcharias* and numerous others which form thick enamel of comparatively complex structure, and the ameloblasts are enormous at the date of their functional activity, in *Raia*, in which the enamel is thin and not unlike mammalian enamel in appearance, the fibrillar layer is also thin, and the ameloblasts only attain to 48μ in length.

And it does not make the least difference so far as the facts here enumerated are concerned whether the tooth is to consist, as in *Carcharias*, of ortho-dentine, or, as in *Lamna*, of osteo-dentine: in either case the calcification commences away from the surface and along the line between the fibrillar layer and the deeper part of the dentine-papilla. The facts above mentioned have been partly described by other previous observers, but they have not been put together, nor their bearing appreciated. But it is interesting to note that Nickerson (8), in describing the development of the scales of a ganoid fish, had written :—" What is very curious in their development is that, although by the increase of the dermis in their neighbourhood a sort of papilliform eminence projecting up into the epidermis is formed, the calcification of the scale takes place, not at the line of junction of the two, but well in the substance of the dermis, of which a thick layer intervenes between the epithelium and the outer surface of the forming plate," though he goes on to misinterpret their ultimate product. It is obvious that he had under observation a precisely similar process, though in the then state of knowledge he misinterprets the nature of the ultimate product, denying the relationship of the outer hard layer to enamel on the ground that it is mesoblastic in origin.

It is evident, therefore, in so-called ganoid or elasmobranch fish the enamel one has to deal with is a tissue which is in a sense hybrid and upsetting to one's previous conceptions.

Both the mesoblastic dentine-papilla and the epiblastic enamel-organ have contributed to its formation, and it is open to argument what it shall be called, though from reasons already given (p. 63) on the balance of its characters it may be regarded as enamel.

Every grade exists between it in its most aberrant forms and the enamel of *Raia*, which latter no one, apart from the knowledge of these facts, would for a moment have hesitated to describe as enamel.

If an endeavour is made to reconcile these different methods of enamel formation and to place them in their proper relation to one another, some difficulty must arise. Provisionally they may be grouped thus :—

(A.) Enamels which are not wholly epiblastic.

These are laid down by the operation of epiblastic ameloblasts in a matrix which is derived from a modification of the surface of the mesoblastic dentine-papilla.

(B.) Enamels which are wholly epiblastic.

(1.) The ameloblasts lose their integrity early and are transformed into a delicate stroma in which enamel calcification goes on, *e.g.*, *Gadidæ*, *Labrus*, *Sargus*, and no doubt many others.

(2.) The ameloblasts persist throughout the whole period of enamel formation and are not bodily transformed into a stroma. Their free ends are, however, continued into long processes which during enamel formation run through the whole thickness, and some of them remain uncalcified. This has been worked out only in marsupials, though doubtless other tubular enamels, such as that of *Hyrax*, *Jerboa*, shrews, &c., are similarly formed.

(3.) The ameloblasts persist through the whole period, and the processes of their free ends pass only a short distance into the forming enamel, full calcification following very closely upon the heels of any alteration. This obtains in all placental enamels which are not conspicuously tubular.

It will be observed that the above grouping shows an increasing specialisation and importance of the ameloblasts, which at first only take a share in the result and afterwards effect the whole process unaided. But the gaps are wide, and it may be expected that further research may reveal the stages by which the dentine-papilla surrendered its share in the process.

THE DENTINE-ORGAN.

The dentine germ, or dentine-bulb, of which the origin has been already described, at first was nothing more than a part of the mesoblastic myxomatous tissue of the jaw which had become richer in vessels and cells than other neighbouring parts, but which did not present any structures essentially different from those found around it. It very speedily assumes the form of the apex of the future tooth, becoming, if it be a canine, simply conical (it has, however, been alleged that the canine papilla has at first a hint of two cusps, thereby showing its relationship to the premolars); if a tooth with two cusps, bicuspid, &c.

At an early stage the cells of the surface of the dentine-papilla in no way differ from those which lie deeper (Fig. 120). But as the time approaches for the commencement of calcification a more highly specialised layer of cells, which will ultimately form the surface, begins to be differentiated (Fig. 121).

These cells, probably largely concerned in the formation of the dentine, form a very distinct layer, which, after the commencement of calcification, adheres more strongly to the formed cap of dentine than to the rest of the pulp, and so is often pulled away with the former when the two are separated ; hence this layer of cells (odontoblasts) has obtained the name of *membrana eboris*, or membrane of the ivory ; but the student must beware of falling into the mistake of supposing that it really is a " membrane " properly so called.

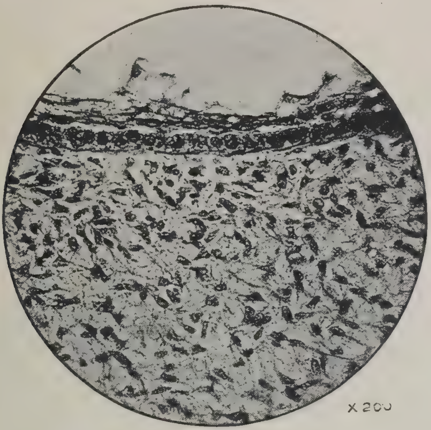

FIG. 120.—Surface of pulp of young tooth-germ. A layer of ameloblasts not as yet fully developed covers the surface ; the surface cells of the pulp are not yet differentiated, so that no indication of the odontoblast layer is seen. (After Dr. Paul.)

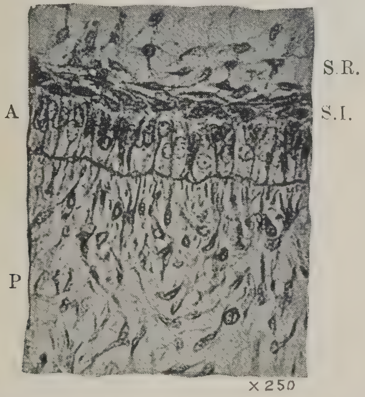

FIG. 121.—From above downwards are seen the (S.R.) stellate reticulum, (S.I.) cells of the *stratum intermedium*, (A.) the ameloblasts, and (P.) the dentine pulp. Near to the surface of the latter the cells are assuming a direction perpendicular to the surface, and the odontoblast layer is beginning to be indicated. (After Dr. Paul.)

The origin of these cells has been carefully described and figured by Paul, who points out that some dentine matrix begins to be formed before they are by any means completely differentiated.

Calcification of the Dentine.—The dentine is formed upon the surface of the dentine-bulb, or papilla, from without inwards, so that no portion of dentine once calcified can receive any increase in external dimensions; all additions must take place upon the interior of the dentine cap. The nature of the dentine-bulb has already been to some extent described; it remains to consider somewhat more minutely the histological features of its surface.

The cells constituting the *membrana eboris*, to which Waldeyer has given the convenient name of "odontoblasts," form an exceedingly sharply defined layer upon the surface of the dentine, being arranged in a single row; the cells immediately beneath them differ strongly from them, so that there is not so marked an appearance of transitional structure as may be seen in the *stratum intermedium* of the enamel-organ. Nothing whatever like the linear succession of formative cells, which, by coalescence at their ends, went to form the dentinal tubes, as described by the older writers, is to be seen.

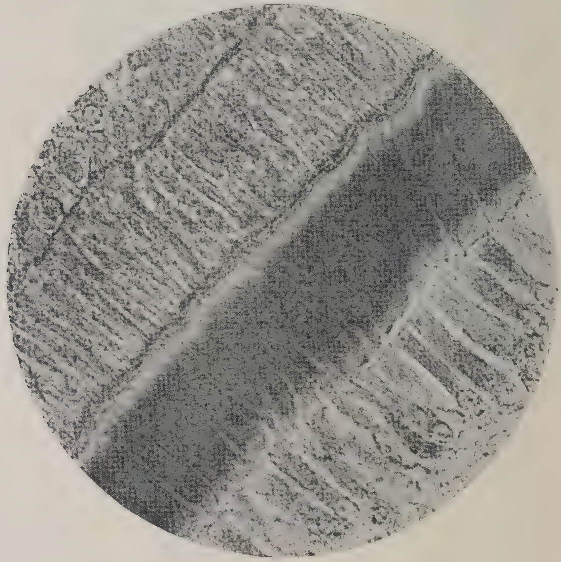

FIG. 122.—General view of tissues at the time when a thin layer of dentine has been formed; from a photograph given to the author by Leon Williams. At the top, to the left, is seen the *stratum intermedium*, next the ameloblasts, then young dentine, and, below, the odontoblasts, which may be seen sending processes into the young dentine.

The odontoblast cells vary in form according as the dentine formation is actively going on or not, but at the period of their greatest activity they are broad at the end directed towards the dentine cap, so as to look almost abruptly truncated. The several processes of the cells have already been described; there are, however, sometimes several "dentinal processes" proceeding from a single cell, and Boll has counted no less than six.

The cells are finely granular. The nucleus is oval, lies in that extremity of the cell which is farthest from the dentine, and is sometimes prolonged towards the dentinal process so as to be ovoid or almost pointed.

The peripheral process passes into the tubes of the dentine, and it frequently happens that, when the *membrana eboris* is only slightly separated from the dentine, these processes, which constitute the dentinal fibrils, may be seen stretching across the interval in great numbers.

The odontoblasts, as may be seen from Fig. 81, are placed rather closely together, and there is not very much room for any other tissue between them so long as the formation of dentine is actively going on. Prior to its commencement, however, the cells are not so square at their ends, and the appearance of the extreme edge of such a pulp suggests the idea that they are embedded in a transparent and structureless jelly, which projects a little beyond them.

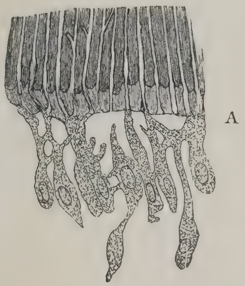

FIG. 123.—Odontoblasts *in situ*. (After Waldeyer.) This figure also shows at A. a layer of formed matrix not yet calcified. The pulp processes are not illustrated.

When the pulp has completed, for the time being at all events, the formation of the dentine, the odontoblast cells become more elongated and more rounded in their outline and taper off towards and into the dentinal process, instead of having truncated ends.

Several more or less divergent views as to the exact method of development of the dentine have from time to time held the field, the question turning mainly upon the part played by the odontoblasts. The close relation of these cells to the dentine, their change in form according as dentine-building is or is not actively going on, and the absence of any other of the large cells which elsewhere are associated with the elaboration of special products, would naturally lead to the inference that they are the chief factors in the segregation of calcium salts and their incorporation in the dentine, a view which has obtained many adherents.

According to this view, which is supported by Waldeyer, Frey, Boll, Lionel Beale, and many other of the older writers, the dentinal fibrils, the dentinal sheaths, and the matrix between these latter, are alike derived from the metamorphosis of the odontoblast cell. In other words, the three structures in question may be considered as being three stages in the conversion of one and the same substance: thus there is the dentinal fibril in its soft condition, little more than the unaltered protoplasm of the cell; then the dentinal sheath, one of those peculiarly resistant substances which lie on the borders of calcification; and lastly, the matrix, the completed, wholly calcified tissue.

Thus, it has been supposed that the most external portions of the odontoblasts undergo a metamorphosis into a gelatigenous matrix, which is the seat of calcification, while their most central portions remain soft and unaltered as the fibrils. Intermediate between the central permanently soft fibril and the general calcified matrix is that portion which immediately surrounds the fibril, namely, the dentinal sheath.

This view differs but little from that of von Ebner and Röse, which, however, is to some extent intermediate between the older theory and that advocated by Mummery: they believe that the whole of the dentine is derived from the odontoblasts, but that while their axial portions persist as dentinal fibril, their peripheral portions become metamorphosed into a delicate fibrillar gelatigenous tissue, a connective tissue in fact, which, forming the matrix, receives an impregnation with calcium salts.

Just as in the case of enamel, there are writers who hold that the odontoblasts do not themselves become calcified, but that they preside over the secretion of a material which is converted into dentine. Thus Kölliker and Lent believe that while the canals and their contents are continuations of the odontoblasts, the matrix is a secretion either from these cells or from the rest of the pulp, and so is an "intercellular" substance. Their view is therefore intermediate between the excretion and conversion theories; and Kölliker goes on to say, "Since the dentinal cells are immediately drawn out at their outer ends into the dentinal fibres, and do not, as was formerly thought, grow out in such a manner that the dentinal fibre is to be regarded only as the inner part of the cell, so it is not possible to derive the dentine immediately from the cells." But is not Kölliker thinking and writing of those aged, spent cells which his pupil Lent figured? No one could speak of a young, active odontoblast as "drawn out into the dentinal fibril." A properly prepared section of young developing dentine shows that the cells are square and abrupt towards the dentine; they do not taper into the dentinal process in the smallest degree, and there is little room for any intercellular substance.

Hertz coincides with Kölliker in regarding the matrix as a "secretion from all the dentinal cells in common, which stands in no definite histological relation to the individual cells," but his figure also probably is representative of an adult inactive surface of pulp, in which dentine formation has almost ceased.

Kölliker and Lent are of opinion that a single cell is sufficient to form the whole length of a dentinal fibril, not having seen evidence of active cell growth in the subjacent layer of the pulp, from which they could infer that the *membrana eboris* was supplemented by new cells from below. In a later edition of his work, however, Kölliker speaks with much more hesitation on this point.

Magitot held that the whole of the dentine is "a product elaborated by the odontoblasts," but neither secreted by nor formed by the conversion of the odontoblasts, and he denied the existence of the sheaths of Neumann *in toto*.

Klein believes that the odontoblast forms the matrix only, whilst the dentinal fibrils are processes continued up between the odontoblasts from a subjacent layer of stellate cells.

Robin and Magitot formerly held that the dentine matrix was formed by the transformation of the odontoblast cells, but that the tubes were *interspaces* between these latter, not corresponding with the axes of the cells.

Baume (³) holds that the odontoblasts secrete a material which calcifies rather than that they are themselves converted.

And Hopewell-Smith believes that the odontoblasts take no part in the formation of the matrix of dentine, which is furnished by smaller cells near the pulp surface.

It will be remembered that von Ebner has shown the existence of a delicate fibrillar structure both in bone and in dentine; and his investigations have been carried further by Mummery (⁸ᵃ), whose view, briefly expressed, is that the dentine matrix is due to a calcification in a delicate connective tissue which has not been derived from the odontoblasts at all, but from the general connective tissue of the pulp, *i.e.*, that the dentine matrix is of an *inter*-cellular nature. He confirmed von Ebner's observation that in the completed matrix now and again traces of a much-masked fibrillar structure were to be found, especially in teeth which had undergone the slow decalcification attendant upon the early stages of dental caries. But he further showed that by the use of Koch's method as modified by Weil a connective tissue was to be demonstrated in the periphery of the pulp, which connective tissue apparently ran continuously into the matrix, somewhat as Sharpey's fibres run into bone.

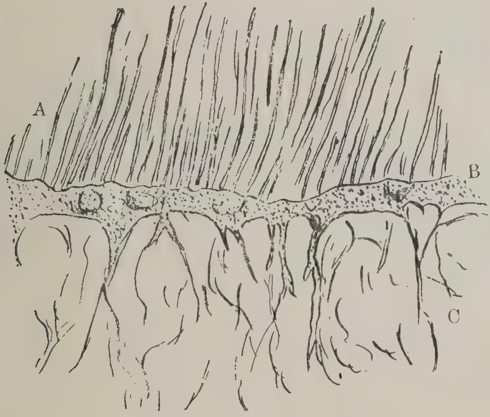

Fig. 124.—Longitudinal section at apex of radical portion of pulp in human premolar, showing odontogenic fibres in continuity with the dentogenetic zone. × 350. At A is seen the formed dentine; at B a layer of forming dentine, the "dentogenetic zone," to which a number of connective tissue bundles (C) adhere. (After a drawing by Howard Mummery in the "Phil. Trans. Roy. Soc. Lond.")

According to him, dentine is developed very much like a membrane bone, there being, however, this difference : that in the case of dentine long protoplasmic processes from each odontoblast cell persist, though the cells themselves do not become enclosed in the forming tissue. In the case of bone, some of the osteoblasts do become invested and persist as the branched cells which occupy the lacunæ. He has traced these connective tissue bands passing between the odontoblasts and running into the dentine, while, on the other hand, their continuity with the general connective tissue of the pulp is easily demonstrable. They are, however, not well seen in sections which run exactly in the plane of the length of the odontoblasts, which in that case are apt to obscure these very delicate fibrils somewhat ; and there appear to be cells applied to these bundles of connective tissue which are distinct from the odontoblasts, and recall the cells upon the osteogenetic fibres of bone.

For the details of the reasons which have led him to adopt this view, the reader must refer to his original paper ; but a very strong argument in its favour is derived from a study of the development of vaso-dentines.

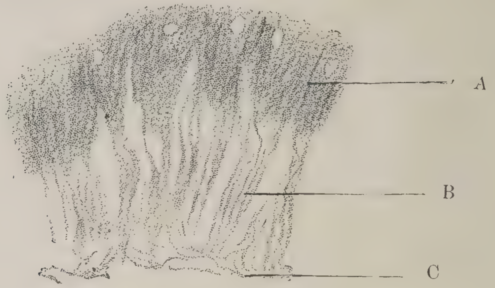

FIG. 125.—Decalcified section of tooth of hake. A. Formed dentine. B. Connective tissue bundles running into it without break of continuity. C. Connective tissue framework of the pulp.

In the latter there can be found a very distinct layer of straight parallel fibres which abut upon the forming dentine. They really are a layer of specially arranged connective tissue fibres. For their nuclei are inconspicuous, and they quite lack the fully developed appearance of true odontoblasts.

Though they so far resemble them as to pull away in a continuous sheet adherent to the dentine, and of perfectly uniform thickness, yet in suitable preparations they can be seen to be continuous with the connective tissue framework of the pulp, which in vaso-dentine pulps is far more strongly developed than it is in the pulps of orthodentine.

There being no dentinal tubes to mask it, the dentine can often be seen splitting up in decalcified specimens into bundles of the same size as the fibres of the pulp layer.

Moreover, it is much more easy to see the fibres alluded to running into the formed dentine matrix on the one hand, and on the other into the connective tissue deeper in the pulp in vaso-dentine than in hard tubular dentine.

In the peripheral or first-formed part of the dentine of many vaso-dentine teeth there is a structure which might almost be termed a petrifaction of the connective tissue stroma unchanged. This is well seen in Fig. 126B, drawn from the tooth of a cod. It cannot be said that there is any fundamental difference between the development of a vaso-dentine and that of ortho-dentine, for the very same tooth may be composed at one part of the one and at another of the other, as is well exemplified in the tooth of a flounder (see Fig. 71), so that it is quite safe to use the one tissue as illustrating the development of the other.

Fig. 126A.

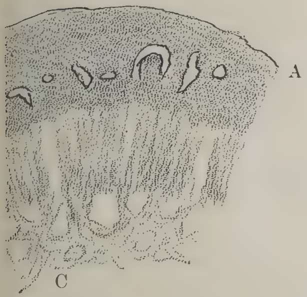

Fig. 126B.

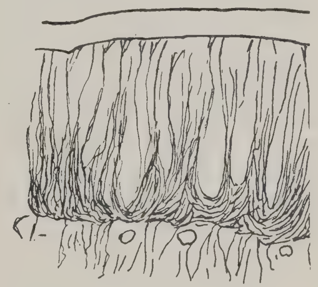

Fig. 126A.—Decalcified section from a hake. The connective tissue fibres are seen forming a layer as distinct as, though greatly thicker than, an odontoblast layer. In the formed dentine at A the vascular canals are seen, and at C the general connective tissue stroma of the pulp.

Fig. 126B.—Outer layer of dentine of a cod.

If then it be true, as it appears to be, that the dentine matrix is formed in a connective tissue basis, it becomes a question what share the odontoblasts take in the process. It may be taken as certain that the odontoblast is concerned in the development of the dentinal tubes, keeping them open, as it were, by its process, the dentinal fibril; and it seems clear that the same odontoblast forms the whole length of the fibril, itself receding backwards as the dentine grows; it seems also possible that it is concerned in the development of the sheaths of Neumann. But inasmuch as Mummery believes that he has seen other cells applied to the connective tissue fibres, both in man and in fish, if he is right, it becomes doubtful whether the odontoblasts alone are concerned in elaborating the calcifying material.

On the whole, however, their general resemblance to the layers of osteoblasts which clothe the surfaces of developing bone renders it probable that they are active agents in the development of the dentine, and it is certainly known that dentinal tubes are not formed in their absence ([12a]).

It has been mentioned (p. 106) that the different varieties of dentine merge into one another, and that also dentine in some of its varieties is not distinguishable from bone. The connective tissue theory of its development therefore derives no little support from comparative anatomy, for it brings the development of dentine into line with that of bone, and, on the other hand, with that of structures very like dentine, which occur in the endo- and exo-skeletons of a great many fish. But other views are still entertained by some authors.

There is another feature in the development of dentine which has not so far been alluded to. During the period of active growth of this tissue, but not afterwards, there is a layer between the odontoblasts and the completed dentine, which appears to be in a transitional stage. This, the dentogenetic zone, usually takes the stain much less deeply, or, in the case of double staining, takes a different colour from that of the rest of the dentine when this has been decalcified. In sections prepared by Weil's process it stains more deeply than the dentine. In this layer an appearance of striation, parallel to the surface of the pulp cavity, can sometimes be seen, and these striæ can be faintly seen in the completed dentine near to it.

In this connection it is interesting to note that decalcified dentine sometimes splits up into laminæ concentric with the pulp, and F. J. Bennett noted that in teeth long kept in glycerine, which has a slowly decalcifying action, a similar splitting occurred. The layer of incomplete dentine is, like Neumann's sheaths and the contents of interglobular spaces, stained a deep black by Golgi's method of using nitrate of silver.

The thinnest layer of dentine, such as may be found at the edges of the dentine cap, is soft and elastic, and so transparent as to appear structureless. Where it has attained a somewhat greater thickness, globules begin to appear in it, which are smaller in the thinner and larger in the thicker portion of the dentine cap. As they are actually in the substance of the cap, their growth and coalescence obviously go on without any very immediate relation to the cells of the pulp; in point of fact, a process strictly analogous to that demonstrated by Rainey and Professor Harting (see p. 160) is going on. Thus in the formation of the first layer of dentine a stage of metamorphosis preparatory to impregnation with calcareous salts distinctly precedes that full impregnation which is marked by the occurrence of globules and their subsequent coalescence. The occurrence of these globular forms, and consequent large interglobular spaces, in the deeper parts of adult dentine, is therefore an evidence of arrest of development rather than of any otherwise abnormal condition.

When the formation of the dentine and enamel has gone on to the extent of the crown of the tooth having attained its full length, the reproduction of new formative pulp (in teeth of limited growth) takes place only over a contracted area, so that a neck, and finally one or more roots, are the result of its conversion into tooth substance. In teeth of constant growth, however, no such narrowing of the formative pulp takes place, but the additions to the base of the tooth are of constant or ever-increasing dimensions, as in some tusks, which are thus conical in form.

Little is known as to the rate of increase of teeth of persistent growth, nor as to whether this increase is constant or intermittent. But the tusk of a walrus which was in the possession of the late Professor Charles Stewart seems to distinctly indicate that its growth was intermittent. This tusk has over a considerable part of its surface been severely weathered, a small portion having been protected. The protected surface is smooth and in no way unusual, but the weathered portion bears circumferential rings slightly more prominent than their interspaces. Towards the apex or younger part of the tooth these are about an inch apart, but the interspaces diminish with regularity towards the base, where at last they attain a fairly constant separation of about a third of an inch. They can hardly be due to anything else than intermissions of growth, and each interspace probably represents the annual increment, large while the tooth was young and, as the creature grew older, short and subsequently smaller.

It is said that the number of roots which would have been developed at the base of a particular dentine organ may be inferred from the vessels, *i.e.*, that in a single-rooted tooth the vessels would, even at an early period, form a single fasciculus ; in a double-rooted one, similarly, they would be arranged in two bundles, so that the ultimate formative activity will be exercised around one, two, or three centres of nutrition.

Aitchison Robertson found by feeding rabbits with madder that about 1 mm. a week was added to their incisors, but that their molars increased more slowly. The rate of growth of human dentine has not been accurately determined, but the tables of Magitot and of Röse indicate a far slower rate of addition than this (cf. p. 204).

There is some reason to think that dentinal tubes once formed are possibly capable of further calcification, by which their calibre becomes sensibly diminished. Thus Sir John Tomes, speaking of the incisor teeth of rodents, states, " The tubes which proceed from the pulp cavity near the base of the tooth are, in most cases, perceptibly larger than those that are situated higher up ; hence it follows that, as the latter were once near the base of the tooth, the dentinal tubes undergo a diminution of calibre after their original formation. In the teeth of the *Sciuridœ* I have found a difference of size amounting to a third or half between the tubes near the base and those near the surface in wear."

Lionel Beale calls attention to the fact that the hollows of the canals are larger nearest to the pulp, and smallest at the periphery of the tooth, in other words, at the oldest part; also that calcification is still slowly going on even in advanced life, so as often to lead to the obliteration of the peripheral tubes. There is, too, the statement of Robin and Magitot, that the teeth become more rich in calcareous salts as age advances, so that analyses of human teeth show great discrepancies.

It is difficult to see how a dentinal tube once formed can become contracted to a third or half of its diameter unless it is believed that that which was at first the soft tissue (dentinal fibril) occupying its canal may become at its periphery metamorphosed into "dentinal sheath," while that which was originally this latter has passed into the condition of matrix. But it has been urged (see p. 78) that the dentinal sheath has no separate existence in the dentine until after its disintegration by a strong acid.

The explanation has, however, been suggested that the odontoblasts and their processes differ in size during different periods in dentine formation (Hopewell-Smith); and probably in this observation lies the whole truth of the matter.

Calcification of Vaso-dentine.—Like ortho-dentine, this is developed in a uniform layer upon the surface of a simple pulp, which can be pulled out of the cap of formed dentine at any time.

During the calcification of ordinary dentine there is an abundant plexus of capillary vessels a very short distance beneath the odontoblast layer, but this recedes as dentine formation goes on, and does not, except as a matter of accident, get included in the forming dentine. Nevertheless, a moment's reflection will show that (except in the earliest stages, before any dentine is formed) this plexus must at a prior time have occupied the place now taken possession of by the inward-marching odontoblasts and dentine. But in the calcification of a formative pulp into vaso-dentine this recession of its vessels before the advancing border of calcification does not take place; the whole vascular network of the papilla remains and continues to carry blood circulating through it, even after calcification has crept up to and around it.

Just as in a hard dentine, the calcification takes place on the surface of the pulp, but owing to the great development of the connective tissue elements, the odontoblasts are not so conspicuous, although, by search, round cells like osteoblasts are to be found there.

Indeed, as has already been seen, the very same pulp with an odontoblast layer is able, at the tip of the tooth, to form a finely tubular dentine, and lower down to gradually change its methods so as to leave vessels carrying red blood through special channels (see Fig. 71). The typical odontoblasts seem to be concerned in keeping open the tubes of dentine, in which their protoplasmic processes remain.

The capability of a pulp to change its method of calcification is very prettily illustrated in the teeth of some fish, of which the *Sargus* may be selected.

In this fish the dentine pulp for some time goes on forming a fine-tubed hard dentine in which no vascular canals exist, but at a certain point a sudden break occurs, which (Fig. 127) coincides with the commencement of the implanted portion of the tooth.

This implanted portion differs from the true dentine tooth above it, in that it contains at first a few, and then no, dentinal tubes at all, and it does contain vascular loops and the somewhat irregular spaces which are to be found in the bones of these fish. Moreover, at the base of the tooth above the break, towards the outer surface of the dentine, a few vascular loops begin to appear, foreshadowing the more complete change which is about to occur (Fig. 74).

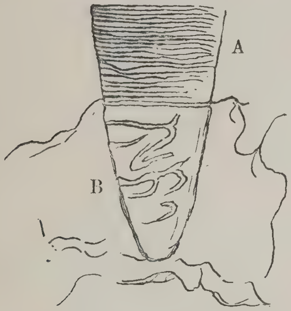

Fig. 127.—Base of the dentine of the crown, and the implanted portion of the tooth of *Sargus*. The surrounding bone in which the latter is imbedded is indicated in outline only. A. Fine-tubed dentine. B. Vaso-dentine.

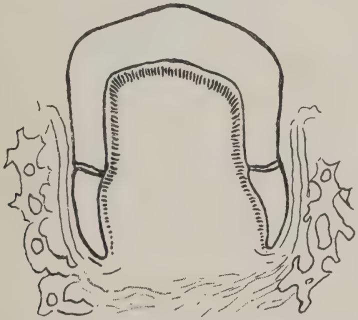

Fig. 128.—Diagrammatic representation of tooth and tooth-sac of *Sargus*, showing the relation of the implanted portion to the odontoblast layer and the tooth-sac.

The great peculiarity of the process is that there is no apparent change in the structure of the formative pulp, which is continued down with its odontoblast layer just the same, not the smallest difference being distinguishable between the pulp above and below the break. Below it, the tooth pulp with its odontoblast layer goes on at first forming an additional portion of the same diameter as before, but it is thinned down pretty speedily to an edge.

The after-history of this deeper portion of the tooth is that it is imbedded in and thoroughly fused with the surrounding bone of the jaw.

Calcification of Osteo-dentine.—With the exception of the thin external layers (see Fig. 77), which are developed from a superficial layer of not very highly specialised cells, osteo-dentine is built up in a manner fundamentally different from that in which ortho-dentine, plici-dentine, and vaso-dentine are constructed.

For it is not, like these, a surface formation ; it is not laid down in a regular manner upon the exterior of a pulp, and it has no relation to an odontoblast layer, if, perhaps, its thin exterior shell be excepted.

So soon as this has been formed, its inner surface becomes roughened by trabeculæ shooting inwards into the substance of the pulp, which speedily becomes traversed completely by them, as well as by the connective tissue bundles which are continuous with them. Thus the pulp, being pierced through in every direction by these ingrowths, cannot be withdrawn, like the pulp of a hard or of a vaso-dentine tooth, from the interior of the dentine cap. Osteoblasts clothe, like an epithelium, the trabeculæ and the connective tissue fibres attached to them, and by the calcification of these the osteo-dentine is formed.

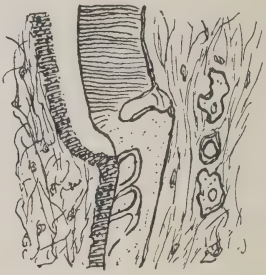

Fig. 129.—Point of junction of the two portions, more highly magnified.

The process is exactly like the calcification of any membrane bone, and the connective tissue bundles remind one of those which are believed to be the occasion of the formation of Sharpey's fibres in bone. In the case of teeth which are going to be anchylosed to the subjacent bone, these fibres run continuously from the interior of the dentine cap down to the bone, and calcification in and around them binds the two inseparably together.

It is interesting to note, especially in connection with the fact that some observers believe Sharpey's fibres to be elastic, that the hinged teeth of the pike (see Fig. 151) owe their power of resilience entirely to the elasticity of these connective tissue bundles, which do not become completely calcified, although at an early stage it would be quite impossible to say whether a particular tooth was going to be anchylosed, or to be a hinged tooth with elastic attachments.

Thus it will be seen that if the connective tissue theory of dentine development be accepted, the development of the several varieties of dentine, which seem to run into one another structurally by almost imperceptible gradations, comes into line and so seems more intelligible. Still it may be possible that in each kind, as particularly clearly seen in osteo-dentines, osteoblastic cells, as apart from odontoblastic cells, may produce the dentine matrix.

Dental Follicle.—By the time that calcification is commencing, there is a tooth-follicle or tissue forming a tough capsule-like investment around the dentine-germ and enamel-organ. At an early period of development the tissue forming the dentine-papilla of a mammalian tooth is seen to be prolonged outwards and upwards from its base (see *h* in Fig. 94); these processes appear to grow rapidly upwards, so as to embrace the enamel-organ; but whether this is really so, or whether it is merely that the ill-defined tissue in which the dentine-forming organ has itself originated is in this region also becoming more pronounced, it is hard to say; probably the latter is the more correct. This upgrowth from the base of the dentine-papilla is the first appearance of a special dental sacculus, which is thus derived from sources identical with that of the formative organ of the dentine.

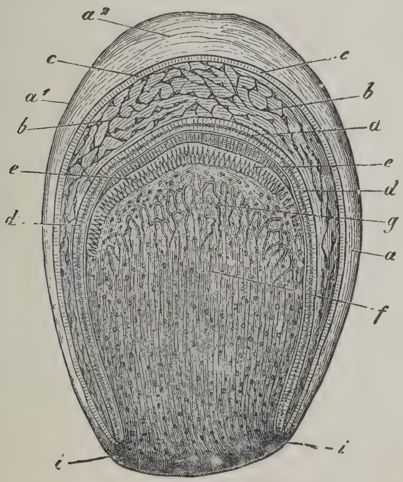

FIG. 130.—Tooth-sac of a calf (semi-diagrammatic). *a*. Tooth-sac. a^1, a^2. Its outer and middle portions. *b*. Stellate cells of enamel-organ. *c*. External epithelium of enamel-organ. *d*. Internal epithelium of enamel-organ. *e*. Odontoblasts. *f*. Dentine pulp or papilla. *g*. Vessels in dentine pulp. *i*. Points where the sac becomes fused with the base of the dentine-papilla.

While these changes are going on, the tooth-sac is becoming

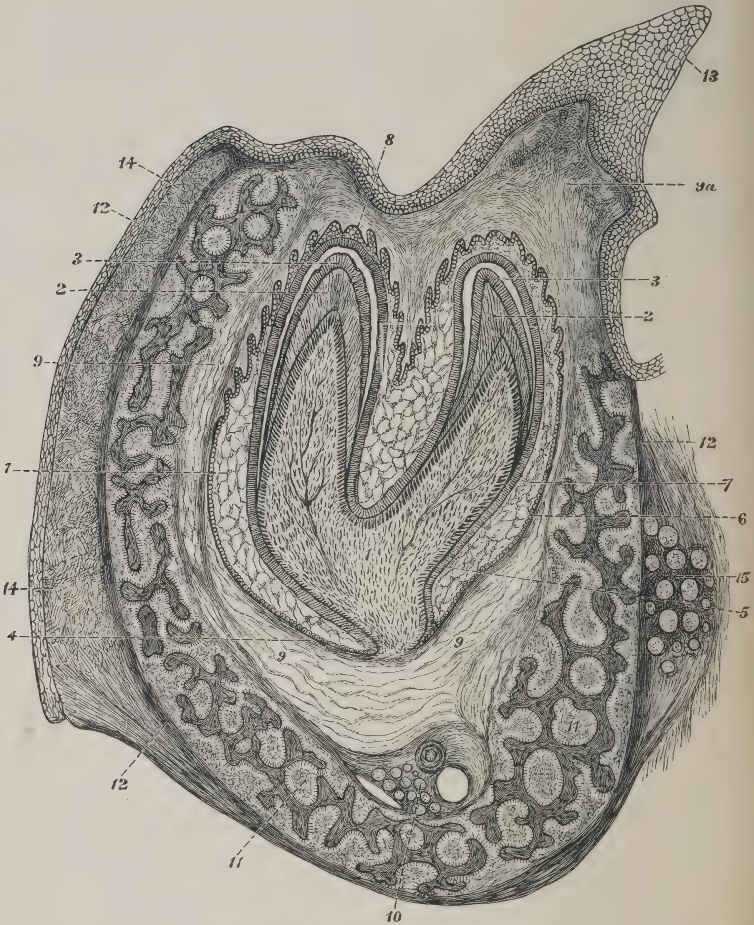

FIG. 131.—Transverse section of the lower jaw and developing back tooth of a lamb, copied from Waldeyer (Henle's "Zeitschrift f. Rat. Med.," 1865). In its outlines the figure is faithful to nature; it is so far diagrammatic that more of the structure than could be seen with the magnifying power employed is introduced.

1. Dentine germ, with its border of odontoblasts. 2. Formed dentine. 3. Formed enamel. 4. Points where the inner epithelium and the outer epithelium of the enamel become continuous. 5. Enamel cells or internal epithelium. 6. External epithelium of enamel-organ. 7. Stellate reticulum of enamel-organ. 8. Papillary projections into the enamel-organ. 9. Connective tissue around the sac, becoming continuous above with that of the gum (9*a*); this constitutes what is called the tooth-sac. 10. Vessels and nerves of the jaw. 11. Bone of lower jaw. 12. Periosteum of the jaw. 13. Heap of epithelium over the young tooth. 14. External skin with its epidermis. 15. Muscular bundles from floor of mouth.

lodged in a widely open gutter of bone, which is being rapidly formed at its sides and under its base. If at this stage (see Figs. 94 and 131) the gum be stripped off the jaws, the developing tooth capsules are torn off with it, and are inseparable from it except by actual cutting, thus leaving the gutter of bone quite bare and empty. In fact, the capsule or sac consists of almost the whole of the connective tissue which intervenes between the special dentine and enamel-germs and the bone, the latter originating deep in the tissues and independently of any periosteum, which is not yet differentiated.

In the first instance the follicle wall is only distinguished from the connective tissue external to it by being somewhat richer in cells, vessels and fibrillar elements, being in fact more condensed or more compact. The sacs, when at their fullest development, are divisible into two layers, an outer thin firm wall and an inner looser tissue, not very dense. At the base of the tooth-sac, the follicle wall is not separable nor distinguishable from the base of the dentine-papilla with which it blends. The follicle wall is richly vascular ; and over the surface of the enamel-organ it is prolonged inwards in the form of villous or papilliform eminences, projecting into the external epithelium of the enamel-organ. To these prominences, which are analogous to the papillæ on the free surface of the gum, some authors attach much importance, as having an influence upon the direction of the enamel rods, and so regulating the pattern formed ; but this view is by no means universally accepted. The internal or softer and looser portion of the follicle wall, which has a consistency but little firmer than that of the stellate reticulum of the enamel-organ, is much developed in ungulates, where there is to be a deposition of coronal cement. This differentiation of a portion of the dental sac is thought by Legros, Robin, and Magitot, to be sufficiently pronounced to justify its designation as a distinct "cement-organ," though many later writers altogether dispute this.

THE CEMENT-ORGAN.

Cementum is, according to these last mentioned authors, developed, just as bone is, in two distinct methods.

Where it is not to be very thick, and is to clothe roots, the ossification takes place in membrane (the alveolo-dental periosteum), but where it is to form a thick layer over the crown, as in ruminants, a cartilaginous cement-organ is formed, and a calcification analogous to formation of bone in cartilage ensues.

Thus the cement-organ is found in those animals only which have coronal cement, such as in some of the *Ungulata*. In a calf embryo about the time that dentine calcification is commencing, there may be distinguished beneath the follicle wall and above the enamel-organ a greyish layer of tissue thick enough to be distinguishable with the naked eye, and of firmer consistence than the enamel-organ, from which it also differs in being richly vascular.

But though it exists at this early period, it is not till later, when, after the completion of the dentine and enamel immediately beneath it, its own function is about to come into play, that it attains to its characteristic structure. This Legros and Magitot designate as fibro-cartilaginous, as there appear in it characteristic cartilage cells, containing one, two, or rarely three cells, which have spherical or ovoid nuclei.

In those creatures which have cementum upon the roots of the teeth only, no special cement-organ exists, but osteoblasts which calcify the cementum are furnished by the tooth-sac.

It is said that the inner layer of the tooth-sac is concerned in the formation of the cement; that the outer layer, conjointly with the surrounding connective tissue, is converted into the alveolo-dental periosteum. In human teeth the parts of the follicle wall or sac cease to be distinctly distinguishable at a comparatively early period, and their importance is not such as to call for any very detailed description.

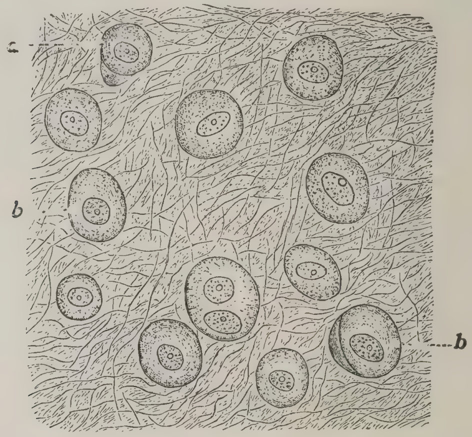

Fig. 132.—Cement-organ of a calf. (After Magitot.) *a*. Fibroid matrix. *b*. Cartilage cells and capsules.

Another structure, once thought important, and now known to be a mere bundle of dense fibrous tissue, is the "*gubernaculum*." Each permanent tooth-sac during its growth has become invested by a bony shell, which is complete, save at a point near its apex, where there is a foramen. Through this foramen, very conspicuous when the surrounding bone is broken away, passes a thin fibrous cord, which is called the "*gubernaculum*," from the notion entertained by the older anatomists that it was concerned in directing or effecting the eruption of the tooth. The gubernacula of the front permanent tooth-sacs perforate the alveolar process of the jaws and blend with the gum behind the necks of the corresponding milk teeth; those of the premolars unite with the periosteum of the alveoli of their deciduous predecessors.

The Calcification of Cementum.—Just as is the case with bones elsewhere in the body, cementum may, perhaps, be formed in two distinct ways—by membranous ossification and by ossification in a fibro-cartilage, the former method obtaining upon the roots of teeth, and the latter upon those crowns where the cement-organ described by Magitot exists.

At the time when the crown of a tooth appears through the gum, it alone is complete, and the root has yet to be calcified: As each portion of dentine of the root is completed, it is coated with a closely adherent vascular membrane which is, in fact, the follicle wall, and which is to become, when the cement is formed, the alveolo-dental periosteum.

The inner or dentinal face of this membrane presents a layer of large cells, the osteoblasts of Gegenbaur, and it is by their agency that bone or cementum is formed. These osteoblasts are themselves a special development where bone is about to be manufactured, as was clearly explained in the following extract from a paper by Sir John Tomes and the late Mr. De Morgan (11), who termed them osteal cells :—

"Here (towards the bone) in the place of cells with elongated processes, or cells arranged in fibre-like lines, we find cells aggregated into a mass, and so closely packed as to leave little room for intermediate tissue. The cells appear to have increased in size at the cost of the processes which existed at an earlier stage, and formed a bond of union between them. *Everywhere about growing bone a careful examination will reveal cells attached to its surface, while the surface of the bone itself will present a series of similar bodies ossified.* To these we propose to give the name of osteal cells."

Behind the osteoblasts and very near to the perfected cementum lies a reticulum or network, which looks like connective tissue, and is confused from the interlacing of the processes. Many of these processes pass into, and are lost in, the clear, structureless matrix of the already-formed cementum, and persist in it as Sharpey's fibres.

Where tendons or ligaments are inserted into a bone, the fibres or bundles of the ligament are continued into the bone as penetrating fibres (Sharpey's fibres). Von Ebner holds that they are composed of bundles of fibre-like connective tissue, and thinks that they are not calcified, but merely imbedded in a calcified matrix. It is more commonly thought that in the development of bone, to which cementum is closely similar, bundles of fibres like those of connective tissue (osteogenetic fibres) appear, and become stiffened and calcified by a globular deposition of calcium salts in them, these globules coalescing.

Thus a membrane-bone is at first a network of spiculæ, beyond which extend the soft osteogenic fibres.

Externally to the fine-meshed network which has been well figured and described by Lionel Beale, the soft tissue surrounding the root partakes more of the character of ordinary fibrous tissue, and may be teased out into fibrils. The fibrous bands run mainly in a direction from the alveolus towards the tooth. Many of them pass through the whole thickness of the soft structures, extending from the bone of the alveolus to the cementum of the tooth, becoming lost at each extremity in the one tissue or the other.

Here and there osteoblasts become enclosed in the forming matrix, and remain as the bone-corpuscle of the future bone, occupying its lacunæ.

In carmine-stained preparations from the teeth of calves a round nucleus may sometimes be seen lying in the stellate "lacuna"; the nucleus soon disappears, and plays no active part in determining the form of the lacuna. The nucleus may also be seen in the developing bones of human fœtuses, and, though this is difficult to understand, the traces of the nucleus seem to be beautifully preserved in the lacunæ of a supposed pterodactyle bone from the Wealden, a section from which was figured by Sir John Tomes in the paper referred to. Exactly as calcification, advancing with irregularity in the interior of an individual cell, fails to render it homogeneous by pervading its whole substance, so it may fail so completely to unite contiguous cells as to obliterate their contours. A lacuna, surrounded by such a contour line, mapping the limits of the original cell, or cluster of cells, is what is termed an "encapsuled lacuna."

That which determines the formation of a lacuna, or an encapsuled lacuna, at any particular spot, is unknown. All that can certainly be said upon the subject is embodied in the following extract from the paper by Sir John Tomes and Mr. De Morgan above alluded to: "We see the boundary of the original lacunal cells only in those cases where the lacunæ have but few, or are entirely devoid of, canaliculi. It would appear to be a law, to which there are few, if any, exceptions, that when anastomosis is established between adjoining lacunæ, the lacunal cells blend with the contiguous parts, and are no longer recognisable as distinct bodies."

The connective tissue-like fibres are not thought by all histologists to be the primary sources of bone matrix, but some regard the fibrillated ground substance as derived from a part of the osteoblasts. Thus Klein considers that the osteoblasts form both matrix and bone corpuscles. "Each osteoblast by the peripheral portion of its cell substance gives origin to the osseous ground substance, while the central protoplasm round the nucleus persists with the latter as the nucleated bone-cell. The bone-cell and the space in which it lies become branched. For a row of osteoblasts a row of oblong or round territories is found, each composed of matrix, and in it a nucleated branched cell. The outlines of individual territories are gradually lost, and a continuous osseous lamina, with its bone-cells, then results. The ground substance is from the outset a network of fibrils; it is at first soft, but soon becomes impregnated with inorganic salts, the process commencing at the 'point of ossification.' The bone-cells, with their processes, are situated in corresponding lacunæ and canaliculi, just as in the adult osseous substance."

Schäfer urges as an objection to this view that there is no indication in the formed bone of the cell areas, nor of partly converted osteoblasts; and if the periphery becomes converted into ground substance and the centre and nucleus persist as the contents of a lacuna, the osteoblast should be far larger than the lacuna, which is not the case. This objection, however, applies with less force to the very large "osteoblast" cell, which is as large as the encapsuled lacuna.

According to Kölliker, the cementum is first deposited in isolated scales, which coalesce with one another, rather than in a continuous sheet. In the teeth of the *Primates*, the *Carnivora*, *Insectivora*, &c., the cementum, at least in any appreciable thickness, is confined to the roots of the teeth.

M. Magitot states that the calcification of the cartilaginous cement-organ of ungulates differs in no respect from that of other cartilages, but in his description he merely states that patches of calcification appear here and there in the deepest portion of the organ, coalesce, and come to invade its entire thickness; and, further, that the cement at the period of eruption is constituted of "osteoblasts" regularly grouped round vascular canals, and included in a ground substance finely striated (6). But where intra-cartilaginous ossifications occur elsewhere in the body a temporary bone is formed by the calcification of the cartilage matrix, which is subsequently absorbed and swept away, as marrow-containing channels appear in it and bore their way through it, substituting for the calcified cartilage a bone developed from osteoblasts; and ultimately all remains of the calcified cartilage or temporary bone disappear. Thus all bone, whether developed in cartilage or in membrane, is formed alike, the calcified cartilage merely forming a temporary framework or scaffolding, in and amongst which the bone is formed from osteoblasts. But M. Magitot does not describe in any such detail calcification of cartilage and subsequent removal to give place to an osteoblast-derived bone, though he speaks of the cartilaginous cement-organ as a transitory or temporary structure.

Historical Survey of the Development of the Teeth.

It may perhaps assist the student, who may be perplexed in endeavouring to reconcile the statements of various authors, to give a succinct history of the views upon the development of the teeth from time to time set forth.

Before the time of Goodsir (1838), the initial stages of development were described by Raschkow somewhat vaguely as proceeding underneath the mucous membrane; he did not, however, trace out in what precise manner the several parts of the tooth-germ originated. The paper of Goodsir giving, in the place of somewhat general notions, a very definite and intelligible description of observations, was accepted without question by most anatomists, if not by all. Accordingly there may be found in all the text-books at and after that period, and in some even up to the present day, the description given by Goodsir reproduced almost without alteration, so that it will be worth while to briefly relate what his views were.

He believed that at an early period in fœtal life there appeared a continuous open groove, running round the whole circumference of the jaws; that from the bottom of this groove there arose isolated and uncovered papillæ, corresponding in number to the milk teeth; that these papillæ became covered in by the deepening of the groove and the meeting of its two edges over them, whilst at the same time transverse septa were formed, so that the several papillæ became enclosed in their own separate follicles. With the details of the process as described by him the reader need not be concerned; it will suffice to remember that he distinguished the four stages: a primitive dental groove, a papillary stage, a follicular stage, and an eruptive stage (the latter of course at a long subsequent period).

Not only were these views accepted quite without question, but they were even extended to explain the development of the teeth in reptiles and fishes, and thus in the Odontographies of Professor Owen and Professor Giebel may be found accounts of development of the teeth in these animals which are perfectly in accord with Goodsir's theory, but which, in fact, are far more inaccurate than the same theories were as applied to mammalian teeth.

Even so careful a writer as Professor Huxley, who was the first to point out that these stages really did not exist either in the frog, the mackerel, or certain other fish, accepted them without question as true of mammals. Markusen * (1849) gave upon the whole a correct account of the process, referring the enamel to the oral epithelium, and Professor Huxley (1854), whilst demonstrating that the stage of free papillæ was not to be found in certain fish and reptiles (a fact also made out in the newt by Dr. Beale), clearly and strongly expressed the same view as to the origin of the enamel-organ, and hence of the enamel. It would be wrong, however, to set small value upon the observations of Goodsir. They were a great step in advance, and were as accurate as the methods of investigation then in use would allow of; moreover, the error in observation is very easy to account for. The epithelium having peeled off as a result of decomposition or the use of weak spirit, the state of things left does not widely differ from that described.

The subject rested for many years without further advances, but in 1863 Kölliker demonstrated, beyond all cavil, the real origin of the enamel-organ and its relations to the oral epithelium, the dentine-organ, and the dental sac.

His views, substantially correct, have been elaborated by Waldeyer, Kollman, Hertz, Legros and Magitot, Wedl, Hertwig and others, and only in minor particulars have they been modified.

The development of the teeth of reptiles was found by a pupil of Kölliker, Santi Sirena, to have several features in accord with that of mammalian teeth; and the author's researches on the teeth of *Batrachia*, fish and reptiles, elsewhere detailed, have proved a striking general similarity in the process throughout the vertebrate kingdom.

Membrana Preformativa.—To the student of dental development few things are more perplexing than the conflicting statements which he reads in various works as to the nature and position of the *membrana preformativa*; after having mastered with difficulty some one description of its character, he finds that many of the most recent authors altogether deny its existence.

According to the older theories of tooth development, under the thrall of which earlier authors have written, the tooth-germ was in the first instance a free, uncovered papilla of the mucous membrane which subsequently sank in and became encapsulated, &c., &c. (see pp. 133 and 201). Moreover, it was taught by the older histologists that fine homogeneous "basement membranes" were to be found in a great variety of situations, amongst other beneath the epithelium of the mucous membrane, and that these were physiologically of much importance, inasmuch as they formed defining limits, through which structures did not pass. As a necessary consequence of these views, it was assumed as a matter of course that the "dentine papilla" must be covered over by a "basement membrane," or *membrana preformativa*.

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* In the *résumé* given by Messrs. Legros and Magitot, before referred to, due credit is not given to the papers of Markusen and Huxley (1849, 1854) (although they are alluded to), and it appears that too much is given to that of Natalis Guillot (1858).

Thus this membrane necessarily intervened between the enamel-organ and the dentine papilla, and hence gave rise to difficulties in the understanding of the calcifying process. Henle considered that evidences of its presence speedily became lost, but that ossification proceeded in opposite directions upon the two sides of this membrane: from within outwards in the case of the enamel, from without inwards in the case of the dentine.

Huxley, starting on the same hypothesis as to its position, namely, that it was placed between the enamel-organ and the dentine-papilla, came to a different conclusion as to its after-fate. Relying upon the fact that a continuous sheet of tissue or membrane can be raised from the surface of the developing enamel (see p. 170), he concluded that this was the original *membrana preformativa*, that it afterwards became Nasmyth's membrane, and that enamel was developed, without the direct participation of the enamel-organ, seeing that a membrane separated the two.

Kölliker strongly affirmed the existence of the *membrana preformativa*, and in the older edition of his Histology held that it became converted into Nasmyth's membrane.

There are thus three situations assigned to the membrane covering the dentine-papilla, or *membrana preformativa*:—

(i.) Between the dentine and the enamel (Henle);
(ii.) Between the enamel and the enamel-organ, *i.e.*, outside the enamel (Huxley);
(iii.) Between the dentine and the pulp (several writers of less authority).

Many writers deny its existence altogether, explaining on other grounds the appearances observed.

Markusen believed that it was nothing more than the part of the papilla first ossified; and Lionel Beale definitely denies the existence of a membrane in any one of the three situations above detailed, as do also Hertz, Wenzel, and Waldeyer.

Robin and Magitot have offered a plausible explanation of the appearance of a limiting membrane over the pulp, which is briefly this: the formative pulp is rich in a clear substance of gelatinous consistency (which, in fact, forms its chief bulk), reminding the observer of the tissue contained in the umbilical cord. This is somewhat more dense towards the surface, where it forms a matrix for the odontoblasts and projects beyond them, so as to appear, in section or at a thin edge, like a sort of varnish to the papilla. From its greater density near the surface, it may become corrugated, and so seem like a folded or torn membrane.

It is difficult to imagine that such a membrane exists upon papillæ formed at such a great distance from the surface as those of the snake or the lizard (Fig. 101); if there be such a membrane, it might be a secondary development upon the surface of the mass of cells which primarily constitute the rudiment of the dentine-papilla, and in that case is not a part of the general basement membrane of the oral mucous membrane; or else it must have been carried in as a sort of *cul de sac* in front of the inward growing process of the epithelium, to which in that case it would belong rather than to the dentine-germ. Neither of these suppositions commends itself as probable; and a still greater obstacle to the acceptance of a membrane in this position is afforded by the structure of marsupial teeth (see Figs. 35 and 111), in which the membrane would be everywhere perforated by the soft contents of the dentine and enamel tubes.

Huber considers that the *membrana preformativa* is a product of the ends of the odontoblasts, which by a coalescence form a continuous sheet,

TABLES OF THE DATES AT WHICH THE SEVERAL STRUCTURES APPEAR IN HUMAN EMBRYOS. ADAPTED FROM RÖSE.

Length of embryo.	Age.	
12—15 m.m.	34—40 days.	First appearance of epithelial inflection. First trace of Meckel's cartilage, but as yet no trace of bone.
17 m.m.	48 days.	The inflection has (according to Röse) divided into the Lippenfurchenleiste and the Zahnleiste. Deepest layer of epithelium has become cylindrical. Meckel's cartilage fully developed, and first traces of bone appear.
2·5 c.m.	9 weeks.	The Zahnleiste shows alternate enlargements and depressions.
3·2 c.m.	10 weeks.	The enlargements are club-like, and the dentine-papillæ are growing into them. Eight papillæ are present.
4 c.m.	11½ weeks.	In each jaw all the ten papillæ are found. The lip groove has deepened by the disappearance of the upper part of the epithelium which filled it.
11½ c.m.	14 weeks.	The milk tooth germs lie like swallows' nests against the Zahnleiste, from which they are now partly pinched off. First appearance of stellate reticulum. Behind the last milk molar the Zahnleiste runs backwards into the mesoderm, without as yet a vertical connection with the surface epithelium above.

		DECIDUOUS TEETH.												
Length.	Weeks.	I_1.	I_2.	C.	M_1.	M_2.	I_1.	I_2.	C.	Pm_1.	Pm_2.	M_1.	M_2.	M_3.
18 c.m.	17	The necks of the enamel-organs of the front teeth are greatly reduced in size, those of the back teeth still broad: Zahnleiste irregularly thickened, and in front fenestrated. The dental groove formed in front of mouth.										Dentine-papillæ formed.		
24 c.m.	20	Dental groove extends to back of mouth. First trace of calcification in the incisors.										Trace of tooth sac.		

30 c.m.	24	In front of mouth much fenestration of Zahnleiste. Trace of calcification in canines and milk molars.					Papillæ embraced by enamel-germ.		First trace of papillæ.			Enamel germ fully developed.		
36 c.m.	29	In the milk molars there is calcification on each of cusps, but these are not yet united with one another.					Trace of tooth sacs.			Zahnleiste thickened.				
40 c.m.	33				Cusps united.						Trace of enamel-germ.	No calcification as yet.		
		Length of Caps of Dentine and Roots.												
	9 months fœtus.	4½ m.m.	4 m.m.	2½ m.m.	2½ m.m.	3 m.m.	No calcification.					Caps on cusps,		
	Child 4 months.	Root, ½ m.m.	5 m.m.	5 m.m.	4—5 m.m.	3—4 m.m.						4 cusps, 1—2½ m.m.	Bud on Zahnleiste.	
	6 months.	Root, 3½ m.m.	Root, 1½—2½ m.m.	Root, ½ m.m.	4—5 m.m.	3—4½ m.m.	Cap, 3 m.m.	Cap, 2½ m.m.	Cap, 1 m.m.			Caps, 2—3½ m.m.	Papillæ.	
	2 years.												4 cusps, cap, 1½—2 m.m.	
	3¼ years.	Root, 11 mm.	Root, 11 m.m.	Root, 11 m.m.	Root, 8—9 m.m.	Root, 6—7 m.m.	Crown complete.	Cap, 7 m.m.	Cap, 8—9 m.m.	Cusps united. Caps, 5—6 m.m.	Cusps separate. Caps, 1—2½ m.m.	Root, 1½ m.m.	Caps, 2 m.m.	End of Zahnleiste thickened.
	5 years.													Papilla of third permanent molar entering its enamel-organ.

and that this by its calcification becomes the granular layer of Tomes, a view which seems most highly improbable.

It must be remembered also that basement membranes have for the most part been found to consist really of flattened cells, and to be very often incomplete and fenestrated. The latest contribution to the subject is in Leon Williams's paper upon enamel. By staining (apparently with Ehrlich-Biondi stain) he has found an appearance of a distinct line of different colour at that end of the enamel cells where they approach the dentine-papilla, and also at their other ends, *i.e.*, between them and the cells of the *stratum intermedium.* Now a difference in colour with a double stain means a difference of chemical or, perhaps, physical constitution or of reaction to a certain extent; but whether this region of difference can be rightly, on that evidence alone, described as a membrane may be doubted, and Leon Williams expresses himself with some caution as to the nature of the stained lines. And Ehrlich-Biondi is a very fickle stain, very slight causes apparently determining a difference. Thus the completely formed and partly formed dentine and enamel will often stain two different colours.

In former editions of this book Magitot's table giving the date of appearance of the various tooth-germs and the size of their calcified caps was given; but in this, as well as in the last edition, Röse's table has been adopted, the latter having shown that in all probability the age of some of Magitot's specimens was not correctly ascertained. Röse has followed His in his determinations of the age corresponding to certain lengths of fœtus, and some of the principal dates thus ascertained are as follows:—

(i.) First appearance of the dental lamina takes place from the thirty-fourth to the fortieth day of intra-uterine life.

(ii.) About the tenth week the anterior eight papillæ form and become imbedded in their respective enamel-organs, the remaining two following in a week or so. The separating of their enamel-germs from the tooth-band begins about the fourteenth week.

(iii.) In the fourteenth week the tooth-band extends beyond the lowest milk molar, and about the seventeenth week the papilla of the first permanent molar becomes developed.

(iv.) In the sixth month after birth the beginnings of the second molar appear.

(v.) At about three and a quarter years the commencement of the third molar is seen.

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CHAPTER VII.

THE DEVELOPMENT OF THE JAWS—THE ERUPTION OF THE TEETH.

At an early period in the development of the embryo there is a single primitive buccal cavity, which is subsequently divided into a nasal and an oral cavity by the palatine plates growing horizontally across it; the pharynx behind the hinder end of the primitive buccal cavity remains undivided.

About the third week in the human embryo the foregut (see p. 2) becomes enlarged in the head region to form the pharynx. The hypoblast which lines it grows transversely outwards on each side at four different levels, these outgrowths being met by corresponding ingrowths of the epiblast from the surface. The bilaminar membranes thus formed at each spot soon become ruptured. Four clefts are thus formed, of which the first is the largest and the fourth the smallest; these pass right through, so as to become actual slits.

The tissues intervening between them become thickened and strengthened, forming vertical bars between the visceral clefts; the same thing happens in front of the first and behind the last, so that there are five bars or visceral arches to the four clefts. In man these clefts are of course transitory structures, and no true slits are formed, but they remain open in fish and some Amphibia, and are familiar to us as the gill-slits of fish. The intervening bars develop vascular filamentous processes which serve for respiration, forming the gills. The fish takes the aerated water into its mouth and expels it through the slits between its gills or visceral arches.

On their inner aspect these arches in fish often carry teeth which in form and structure resemble those in the mouth.*

The visceral arches have, however, a further importance to the student of the development of the jaws, for inside the first visceral arch, that is to say, in front of the first visceral cleft, a cartilaginous bar is developed, which runs round to meet its fellow of the opposite side. This is known as Meckel's cartilage; it starts from the base of the cranium in the immediate neighbourhood of the future ear, and at this end of it two of the auditory ossicles, the incus and malleus, are ultimately formed.†

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* For a more detailed account of the pharyngeal teeth, the reader is referred to a series of papers which appeared in the *Zoologist* by Colonel Shepherd.—Ed.

† The development and morphology of the auditory ossicles is as yet not accurately determined.—Ed.

The most recent work on the development of the maxilla and mandible in man is that by Prof. Fawcett, of the University of Bristol, who has most kindly written the following *résumé* of his investigations :—

" **The Human Maxilla** is developed as a covering bone to the nasal capsule in close connection with the branches—but not the main trunk—of the superior maxillary nerve which lies at first much above the maxilla.

This bone consists of two originally independent elements, the maxilla proper and the premaxilla, either of which may ossify before the other. But in any event incomplete fusion takes place between them at a very early period, so that their original independence is not manifest when viewed from the exterior.

The maxilla commences to ossify in the neighbourhood of the canine tooth-germ and rapidly grows upwards and downwards, inwards and backwards. The upward growth produces a great part—the posterior—of the nasal or frontal process. The downward growth produces the outer alveolar walls ; the inward one, the palatine process, and the backward one, both outer alveolar and malar processes. These parts are visible at the 19 mm. stage.

The anterior dental nerve runs forwards under the palatine process. At a later stage the palatine process increases greatly in height and at the same time grows backwards, leaving a gap between itself and the outer alveolo-malar process through which the dental nerves run.

Still later the palatine process gives off a dependent ridge on the medial side of the milk molar tooth-germs which forms the inner alveolar wall, and about the same time—37 mm.—metaplastic cartilage forms along the alveolo-molar process, but this rapidly becomes converted into bone.

Up to the 30 mm. stage the main trunk of the superior maxillary nerve lies some distance above the very small triangular orbital surface of the maxilla, but at the 30 mm. stage a groove, the infraorbital groove, soon becomes evident, and its walls subsequently close in to form the infraorbital foramen.

During all but the very early stages the height of the maxilla is relatively small, and the orbital surface is only separated from the roof of the tooth sockets by a thin plate of bone.

With the advent of the antrum of Highmore, which is at first an outpouching of the lateral nasal cartilage and long retains its cartilaginous lining, the orbital floor is separated from the alveolar roof, and this separation increases with the age of the bone. At the 100 mm. stage an off-shoot of the lateral nasal capsule which partially encircles the lachrymal duct becomes invaded by ossification and incorporated within the maxilla.

The maxilla is thus derived mainly from membrane, but in part from metaplastic cartilage and in part from the primordial cranial capsule, and by *one* centre of ossification.

The Premaxilla arises by two centres, one the *palato-facial*, which forms part of the hard palate, appears on the face and contributes to the formation of the frontal process of the complete maxilla.

This centre contains the incisor tooth-germs. The other centre to avoid confusion had best be called (as originally by Rambard and Renault) *the subvomeran.* It forms that part of the premaxilla which lies mesial to Stenson's canal, and is only visible from below when the anterior palatine fossa is of large size. It appears normally at the 50—55 mm. stage and soon commences to fuse with the palato-facial centre.

It may be regarded as a covering bone to the anterior paraseptal cartilage.

The premaxilla and maxilla commence to fuse along the outer alveolar wall almost as soon as they are formed ; elsewhere fusion is delayed, as is well known, to a comparatively late period, that between the nasal processes preceding the remainder.

The Human Mandible, the second bone in the body to ossify, being preceded only by the clavicle in that respect, is developed by two centres, one for each half, which, commencing in ' membrane ' in the immediate neighbourhood of the mandibular nerve, gradually involves certain cartilages, one of which is Meckel's cartilage, and the others are cartilages which arise quite independently of Meckel's cartilage, and are not to be considered as parts of the primordial chondrocranium.

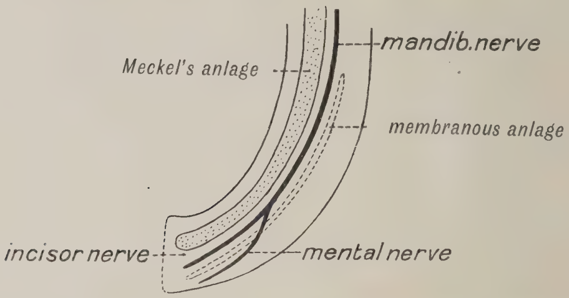

FIG. 133.—Horizontal section of mandibular arch with contained structures at second stage of development.

Ossification in Membrane.—The mandible arises primarily in the interior of the mandibular arch of the embryo which is perforated from back to front by the mandibular branch of the fifth cranial nerve. This nerve on passing forwards divides into two terminal branches, one which runs forwards towards the middle line—the incisor branch, the other which takes a more lateral course—the mental nerve. On each side of the mandibular nerve and its forward continuation, the incisor nerve, the core of mesoblast occupying the mandibular arch condenses to form two denser masses, viz. one median to the nerves in question, the forerunner of Meckel's cartilage, the other lateral to the nerves, the forerunner of the membranous mandible.

The mandibular nerve and its incisor continuation come thus to lie in the interval between the more median Meckel anlage and the more lateral membranous jaw anlage (Fig. 133).

Ossification in membrane commences in the membranous anlage in the angle between the incisor and mental branches of the mandibular nerve at the 17—18 mm. stage; it proceeds backwards underneath the mental nerve, which thus comes to lie in a groove on the upper aspect of the bone (Fig. 134).

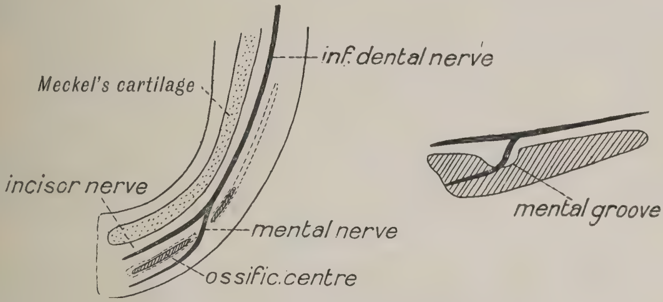

FIG. 134.—Side views of developing mandible.

At a little later stage, just before the 19 mm. stage, the anterior wall of the mental groove forms a spur which grows backwards over the mental nerve, and will at the 19 mm. stage fuse with the hind wall of the groove and so complete the mental foramen (Fig. 135).

During the same period the anterior part of the floor of the mental groove proliferates in an inward direction, insinuates itself between the incisor nerve and Meckel's cartilage, gradually overlapping the latter, by so doing forms the first commencement of the internal alveolar wall, and at a little later date the outer and inner alveolar walls become connected with one another by a bony bridge which, arching over the incisor nerve, forms the incisor canal, the first canal containing nerve to be formed in the mandible (the inferior dental canal containing the inferior dental or mandibular nerve not being formed till the late 60 mm. stage). By the 30 mm. stage there is much advance in growth of the membrane bone, especially in the

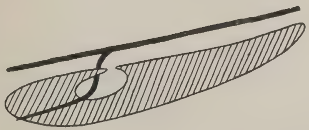

FIG. 135.

backward direction, and the first sign of a coronoid process is now visible.

The condyle region is still in a 'membranous' or connective tissue condition.

In the region near the incisor nerve more active growth is taking place, for two inwardly directed shelves have now made their appearance, one which grows from the inner alveolar wall above Meckel's cartilage, the other from the main mass of bone below the inner alveolar wall which grows inwards below Meckel's cartilage. In course of time these inwardly directed shelves will meet on the medial side of Meckel's cartilage, and enclose it from near the middle line to the region of the second milk molar tooth in the backward direction.

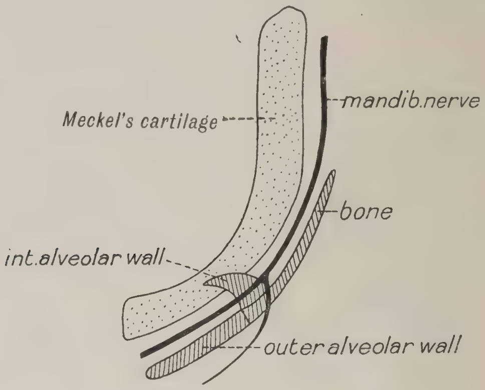
Meckel's cartilage
mandib.nerve
bone
int.alveolar wall
outer alveolar wall

Fig. 136.

In transverse (Coronal) section the appearance is as shown in Fig. 135.

At the 42 mm. stage, Meckel's cartilage becomes invaded by ossification, usually opposite the first and second incisor tooth buds. Prior to doing so the perichondrium becomes markedly thinner opposite these tooth buds, and osteoblasts seem to invade the cartilage opposite the tooth buds from the neighbouring membrane bone. The final result is that Meckel's cartilage undergoes ossification and incorporation in the mandible from near the symphysis to the second milk molar tooth-germ, but *not* by a separate centre of ossification.

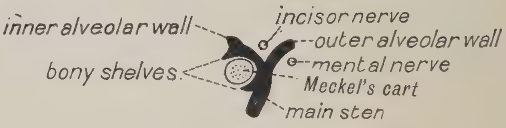
inner alveolar wall
incisor nerve
outer alveolar wall
bony shelves
mental nerve
Meckel's cart
main sten

Fig. 137.

Ossification in other Cartilages.—At a comparatively late period cartilage becomes developed in the unossified connective tissue from which the membranous jaw is formed, and at the following sites :

At the 50—55 mm. stage, a mass of cartilage appears in the region of the condyle (Fig. 138) ; this mass is shaped like a carrot, the large end forming the condyle, the small end tapering away under the root of the coronoid process.

This cartilage is capped at its free end by dense connective tissue which does not chondrify. It is not like ordinary hyaline cartilage, containing very little matrix, and it commences to ossify almost as soon as formed, but it is not completely ossified till quite late, traces being found at birth even. As in the case of Meckel's cartilage, there is no independent ossification, it is simply a case of invasion from the neighbouring membrane bone, and it takes place more rapidly on the inner than the outer side.

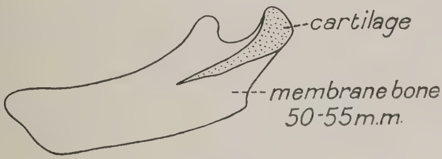

Fig. 138.

At the 80 mm. stage a strip of cartilage of the same nature as the last appears along the anterior border of the coronoid process (Fig. 139). This becomes invaded by ossification from the neighbouring membrane bone.

At the 100 mm. stage a mass of cartilage appears along the top of both the inner and outer alveolar walls (Fig. 140) ; this is continued downwards along the symphysial margin of the mandible and outwards towards the future digastric impression.

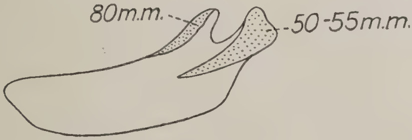

Fig. 139.

It, like the others, is normally ossified by invasion from the neighbouring membrane bone.

All these cartilages are usually classified as metaplastic cartilages, and have no connection whatsoever with Meckel's cartilage, nor are they normally ossified independently. It is possible however that two of them rarely may be, viz., the Coronoid and the Symphysial.

Prof. Fawcett has a specimen of monkey's jaw (species unknown) in which there is an independent bony element in the tip and anterior border of the coronoid process, which corresponds very well with the coronoid strip of cartilage of man, and Kerckringius has described such a mass in man. The writer has never seen it.

It is possible that the *ossa mentalia* which are so often found in the symphysial region are the result of independent ossification of the symphysial cartilage.

Meckel's Cartilage.—This in early fœtal life is a condensation of the mesoblast of the mandibular arch, placed on the medial side of the mandibular (inferior dental and incisor) nerve. Soon it segments off the incus, and developing tumefactions on its posterior end, forms the malleus anlage, the tumefaction producing the head and handle (Fig. 141). The cartilage runs obliquely from behind forward in the mandibular arch, and ends at first some distance from the middle line in a blunt-pointed extremity which has not chondrified when ossification commences in the membranous tissue lateral to it. At a later stage, 24 mm., the anterior extremity of the cartilage begins to swell out so that when it is cut coronally it has a wedge shape.

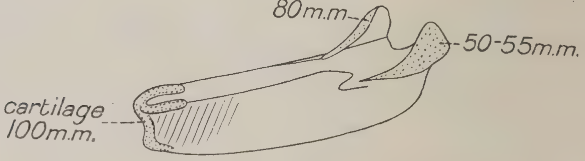

Fig. 140.

The base of the wedge is upwards, and the inner basal angle forms a growing point, which, lying in the loose connective tissue in the symphysial tissue, bends backwards and comes into close contact with its fellow, in some cases even fusing with it as it does in many lower animals, *e.g.*, marsupials. Occasionally this fused point may be segmented off to form an azygos cartilage in the upper part of the symphysial connective tissue, and it is possible that the unpaired *os mentale* which sometimes exists may be derived from independent ossification of this cartilage.

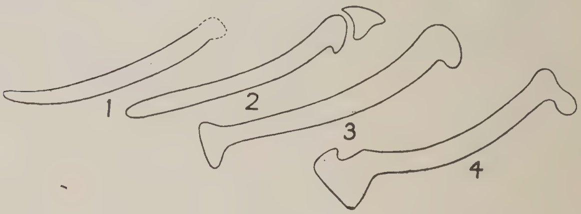

Fig. 141.

Except at the 'growing point' just alluded to, Meckel's cartilage undergoes ossification from the middle line backwards to the region of the second milk molar tooth, and is incorporated with the mandible within the same limits. Behind the tooth-germ in question the cartilage ultimately disappears, but does not become the long internal lateral ligament. That is formed from connective tissue quite independently of the cartilage. During its growth Meckel's cartilage tends to increase in length more rapidly than the membranous jaw; it consequently tends to buckle up behind the region of the second milk molar tooth, and in one case it has been found so bent as to be cut twice in the same coronal section. The perichondrium surrounding Meckel's cartilage is very thick save where it is in close contact with the membrane bone.

In cleft palate and hare-lip the cleft occurs between the endo- and mesognathion; a third dwarfed incisor is sometimes found on the inner side of the cleft, and suggests that the incisor missing from the typical mammalian dentition is I_2.

With the later history of the other visceral arches we have not much concern. It will suffice to note that the second cartilaginous bar, called the hyoid bar, arises very close to Meckel's cartilage, and, indeed, has been considered by some anatomists possibly to participate in the formation of the malleus and incus.

The more usual view is, however, that it in great part disappears, but that it is in part converted into the styloid process, stylo-hyoid ligament, and lesser cornu of the hyoid bone. The bar of the third arch, called the thyro-hyoid, in great part also disappears, but its lower end goes to form the greater cornu of the hyoid bone."

The student who wishes to pursue this subject further is referred to the very excellent and clear account to be found in the latest edition of "Quain's Anatomy."

The later changes which are undergone by the jaws during the development, eruption, and loss of the teeth, have long engaged the attention of anatomists, and amongst others of Hunter, who was the first to arrive at a tolerably correct appreciation of the process. In the first edition of Sir J. Tomes' "Dental Surgery" (1848), the results of a very extensive series of observations carried out upon maxillæ collected by himself were detailed, confirming in the main Hunter's conclusions, but adding many new points to our knowledge; and from this work the author has borrowed largely in the present chapter. The late Sir G. Humphrey, who had overlooked these descriptions, which were never published in any other form than as an introduction to the "Dental Surgery," instituted a series of experiments upon growing animals, which tended towards the same conclusions.

As a means of giving the student a guide in his reading of the following pages, and a clue to the results towards which he is being led, a preliminary statement, which does not pretend to scientific accuracy, may perhaps be useful; while the description given will relate for the most part to the lower jaw, because its isolated position, bringing it into relation with fewer other bones, renders it more easy to study; not that any difference of principle underlies the growth of the upper jaw. The different parts of the lower jaw answer for different purposes, one division of its body having a very close and exclusive relation with the teeth, the other serving distinctly other purposes, as well as forming a base of support for the dental apparatus.

The alveolar portion of the jaw, that which lies above the level of the inferior dental canal, is developed around the milk teeth; when they are lost, it disappears, to be re-formed again for the second set of teeth, and is finally wholly removed after the loss of the teeth in old age.

The portion of jaw below this line, which is essential to deglutition and respiration, is late in acquiring any considerable development. Once formed, it is never removed, save that when in advanced old age the muscles of mastication are no longer in full use it becomes, to a slight extent only, wasted.

In order to understand the drift of the following description, it is essential to keep in view the different life histories of those two parts of the jaw just alluded to.

In an early fœtus, long before the necessity for respiratory movement or deglutition has become imminent, a thin lamina of bone has begun to be developed beneath the tooth-germs, forming, as it were, a semicircular gutter running round the jaw, in which the developing tooth-sacs are lodged. The thin gutter of bone is thus formed above and outside Meckel's cartilage, and intervenes between the rudimentary inferior maxillary vessels and nerves and the teeth. The sides of the bony furrow rise as high as the top of the tooth-germs, but they do not arch over and cover them in in such manner as the permanent tooth-germs are arched in, for the long furrow is widely open at the top.

At the time of birth, the two halves of the mandibles are as yet not anchylosed, but are united only by fibrous tissue.

The alveolar margins are deeply indented with large open crypts, more or less perfectly formed. The depth of these bony cells is only sufficient to contain the developing teeth and tooth-pulps, the former rising to the level of the alveolar margins of the jaws. At this period the crypts or alveoli are not arranged in a perfectly uniform line, nor are they all equally complete. The septa, which divide into a series of cells that which at an earlier age was but a continuous groove, are less perfect at the back than at the front of the mouth. The alveoli of the first incisors of the upper and the lower jaws are a little larger within than at the orifice, and this difference is made still greater by a depression upon the lingual wall of each for the reception of the germ of the corresponding permanent tooth. They are divided from the crypts of the lateral incisors by a septum which runs obliquely backwards and inwards towards the median line. The sockets for the second incisors occupy a position slightly posterior to those for the other incisors, and are divided from the canine alveoli by a septum which proceeds obliquely backwards, and in the lower jaw, as regards the median line of the mouth, outwards. By the arrangement of these divisions the alveoli of the first incisors are rendered broader in front than behind, and these relative dimensions in the sockets of the second incisors are reversed, as shown in Fig. 142. The crypts of the canine teeth are placed a little anteriorly to those

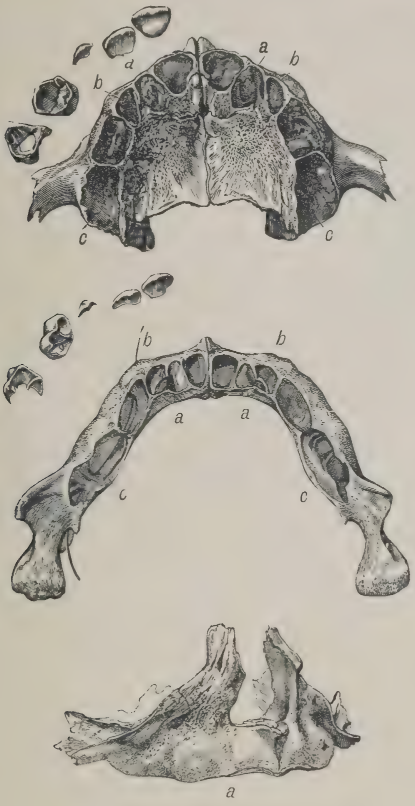

Fig. 142.—Upper and lower jaws of a nine months fœtus, the teeth having been removed from the jaws on one side to show the extent to which they are calcified at this period. (Two-thirds life size.) *a.* Alveoli of second incisors. *b.* Alveoli of canines. *c.* Alveoli of second temporary and first permanent molars. A bristle has been passed through the inferior dental canal.

of the second and nearly in a line with those of the first incisors, giving to the jaws a somewhat flattened anterior aspect.

While the main bulk of the lower jaw is thus made up by the alveoli of the teeth, in the upper jaw the alveoli descend but little below the level of the palatal plates, though the sockets are tolerably deep. The antrum as a special and distinct cavity cannot be said to exist, being merely represented by a depression upon the wall of the nasal cavity, the alveolar cavities therefore being separated only by a thin plate of bone from the orbits.

The figure (Fig. 142) represents also the extent to which calcification has advanced in the various teeth.

A full half of the length of the crowns of the first incisors, about half that of the second, and the tips only of the canines are calcified; the first deciduous premolars are complete as to their masticating surfaces; the second have their cusps more or less irregularly united, in many specimens the four cusps being united into a ring of dentine, the dentine in the central depression of the crown being as yet unformed, and the anterior cusp of the first mandibular premolar. During the formation of the permanent teeth, very similar relations exist between the amount of calcification in the incisors and canines; thus when, as sometimes happens, the development of the teeth proceeds very imperfectly up to a certain date, and then changes for the better, it may be that the lower half of the crown of the first incisor, somewhat less of the second, and the extreme tip of the canine will be honeycombed, while the remainder of the tooth will be perfect, thus perpetuating an evidence of the stages to which each of these teeth had at that particular period attained.

Having noted in some detail the characters of the jaws of a nine months fœtus, we may pass on to the consideration of those changes which precede the cutting of the deciduous teeth. A general increase in size takes place, new bone being developed at all those points where the maxillæ are connected by soft tissue with other bones, as well as from their own periosteum. But the increase in dimensions does not take place in all directions equally, so that material changes of form result.

In correspondence with the elongation of the tooth-sacs, the alveoli become increased in depth, and their edges circle inwards over the tooth-sacs; active development of bone takes place in the sutures uniting the two halves of the jaws to one another, which is compensated by the inclination inwards towards the middle line of the alveoli of the first incisors. In the lower jaw the articular process, at first hardly raised above the level of the alveolar border, grows rapidly up, the direction of the ramus at first remaining oblique, though the angle of the jaw becomes developed as a stout process for the attachment of muscles. At the age of six months the symphysis is still well marked, and the mental prominence first becomes noticeable.

An additional bony crypt for the first deciduous premolar has also appeared, though its separation from that of the second deciduous premolar, from which it was at first in no way distinct, is yet incomplete, especially in the lower jaw. In the upper jaw the first deciduous premolar crypt has no posterior wall; bony cells for the permanent first incisors are well marked, but those for the others are mere deep pits in the palatine wall of the crypts of the temporary teeth.

At the age of eight months, or thereabouts, the process of the eruption of the teeth, or "teething," has fairly set in; anchylosis has taken place at the symphysis of the lower jaw, the mental prominence is well marked, and in the upper jaw the antrum has become a deep depression, extending under the inner two-thirds of the orbit, and thus separating the teeth from the orbit.

Postponing for the moment the consideration of the eruption of the teeth, in order to follow up the growth of the jaws, it becomes necessary to take some fixed points as standards from which to measure the relative alteration of other portions of the bone. In most bones, processes for the attachment of muscles would be very unsuitable for the purpose, because they would alter with the general alteration in the dimensions of the bone; thus a process situated at a point one-third distant from the articular extremity of a large bone will still be found one-third distant from the end, though the bone has doubled in length. The four little tubercles which give attachment to the genio-hyo-glossus and genio-hyoid muscles are not, however, open to these objections, as they are already, so to speak, at the end of the bone, or, at least, of each half of it; and their general correspondence in level with the inferior dental canal, which can hardly be imagined to undergo much alteration, indicates that their position is tolerably constant throughout.

The points selected as landmarks are then the *spinæ mentales*, the inferior dental canal and its orifice, and the mental foramen. The mental foramen itself does undergo slight change in position, but this change can easily be estimated, and may as well at once be mentioned. As the jaw undergoes increase in size, large additions are made to its surface by deposition of bone from the periosteum, necessarily lengthening the canal. The additions to the canal do not, however, take place quite in the line of its original course, but in this added portion it is bent a little outwards and upwards. If we rasp off the bone of an adult jaw down to the level of this bend, a process which nature in great part performs for us in an aged jaw, or if instead we make due allowance for the alteration, the mental foramen becomes an available fixed point for measurement.

The mental foramen, which undergoes most of its total change of position within a few months after birth, comes to correspond with the centre of the socket of the first deciduous premolar; later on it corresponds with the root of the first premolar, which is thus shown to succeed, in exact vertical position, the first deciduous premolar.

On the inner surface of the jaw the tubercles for the attachment of the genio-hyo-glossus and genio-hyoid muscles are in the fœtus opposite to, and very little below the base of the alveoli of the first incisors, a position which they afterwards hold with regard to the permanent incisors. The upper of the two pairs of processes are about at the same general level as the mental foramen.

The general result arrived at by measurements taken from these fixed points is that the alveolar arch occupied by the permanent teeth which have had deciduous predecessors, namely the incisors, canines, and premolars, corresponds very closely with the whole alveolar arch of the child in whom the temporary dentition is complete; and that the differences which do exist are referable, not to any fundamental alteration in form or to interstitial growth, but to mere addition to its exterior surface; or, more briefly, that the front twenty of the permanent succeed vertically to the deciduous teeth, the increase in the size of the jaw in an adult being due to additions at the back in the situation of the true molars, and to the surface.

Thus, if measurements be taken across between the inner plates of the alveoli on either side at the points where they are joined by the septa between the first and second deciduous premolars, and at about the level of the genio-hyo-glossus tubercles, it will be found that the difference is slight, if any, notwithstanding that in other dimensions there is a very great difference between the jaws of a nine months fœtus and of a nine months child.

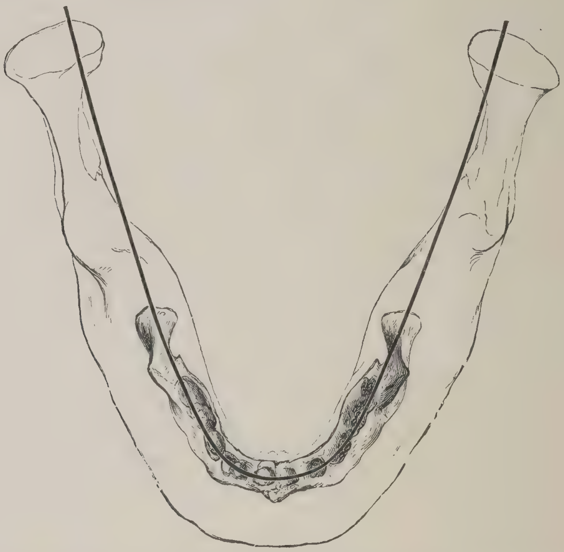

FIG. 143.—Diagram representing a jaw of a nine months fœtus, superimposed upon an adult jaw, to show in what directions increase has taken place.

Again, if imaginary lines be stretched across between these two points, and from their centre lines be drawn forwards to the *spinæ mentales* in the same two jaws, these will be found to differ but little in length in the two specimens.

But if, instead of measuring to the *spinæ mentales*, the line had been carried further to the anterior alveolar plate, a great difference would have been observable; in point of fact, contemporaneously with the development of the crypts of the permanent teeth inside them, the deciduous teeth and their outer alveolar plates are slowly pushed outwards, a process the results of which we see in the separation which comes about between each one of the deciduous teeth prior to their being shed, when the process of dentition is being carried on in a perfectly normal manner.

Measurements taken for the sake of comparing adult jaws with those of an eight months child give closely similar results, which the author has endeavoured roughly to embody in the accompanying figures.

In these it is shown that the increase in the dimensions of the jaw has taken place in two directions: by prolongation backwards of its cornua concomitantly with the addition at the back of the series of teeth of the true molars, which follow one another at considerable intervals of time; and by additions to its exterior surface by which it is thickened and strengthened. The study of the growth of the jaw in vertical depth is also very instructive. We find that, as has already been mentioned, the history of that part of the jaw which lies below the inferior dental canal is very different from that which lies above. From the time of birth to that at which the deciduous teeth begin to be cut, the jaw below that line has been making steady but slow progress in vertical depth; the alveoli, above that line, have been far more active but far more intermittent in their development.

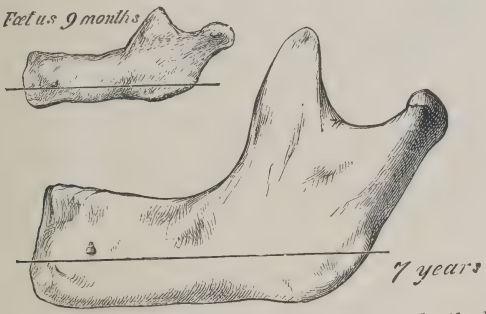

FIG. 144.—Lower jaw of child. The horizontal line marks the level of the inferior dental canal.

Again, passing from the nine months fœtus to the seven years old child, in whom the deciduous dentition is complete, the framework of the jaw below the imaginary line has attained to a depth almost equal to that which it is seen to have in an adult; in the adult again it corresponds pretty well with that in an aged jaw. The alveolar portion, however, is far deeper in the adult than in the child (this difference is not sufficiently well marked in the figure), and in fact constitutes almost the whole increase in vertical dimensions during the passage from the child's to the adult's form of the jaw.

In the lower jaw we may then take it as proven that the basal portion has little relation to the development of the teeth, but that the alveolar, or upper, portion is in entire and absolute dependence upon them, a point to which reference will again be made in speaking of the eruption of the teeth.

It remains to speak in some further detail of the precise means by which the enlargement of the jaw is effected.

To a slight extent there is formation of bone going on at the symphysis prior to complete anchylosis taking place. The share taken by this in increasing the size of the jaw would, however, appear to be but small after the termination of the intra-uterine period. Additions to the surface at the edges of the alveoli and at the base of the jaw are continually going on, and bring about that addition to the exterior already noticed.

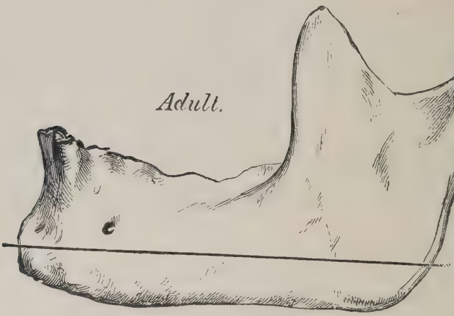

FIG. 145.—Lower jaw of an adult.

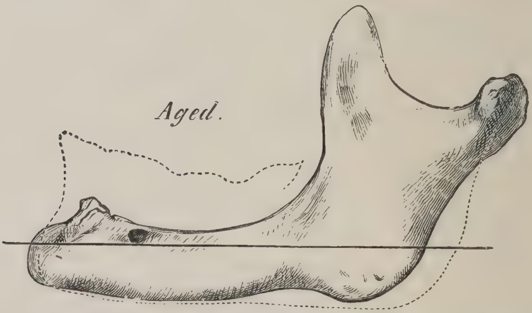

FIG. 146.—Lower jaw of an aged person, the dotted lines indicating the outline of the parts removed by absorption, as the jaw assumes the form characteristic of advanced age.

But the main increase in the size of the jaw has been in the direction of backward elongation; in this, as Kölliker first pointed out, the thick articular cartilage plays an important part. The manner in which the jaw is formed might also be described as wasteful; a very large amount of bone is formed which is subsequently, at no distant date, again removed by absorption; or we might compare it to a modelling process, in which thick, comparatively shapeless masses are dabbed on to be trimmed and pared down into form.

To bring it more clearly home to the student's mind, if all the bone ever formed were to remain, the coronoid process would extend from the condyle to the region of the first premolar, and all the teeth behind that would be buried in its base; there would be no "neck" beneath the condyle, but the internal oblique line would be a thick bar corresponding in width with the condyle. It is necessary to realise fully that the articular surface with its cartilage has successively occupied every spot along this line; and as it progresses backwards by the deposition of fresh bone in its cartilage, it has been followed up by the process of absorption removing all that was redundant.

On the outer surface of the jaw we can frequently discern a slight ridge, extending a short distance from the head of the bone; but if the prominence were preserved on the inner surface, the inferior dental artery and nerve would be turned out of their course. We have thus a speedy removal of the newly formed bone, so that a concavity lies immediately on the inner side of the condyle; and microscopic examination of the bone at this point shows that the lacunæ of Howship, those characteristic evidences of absorption, abundantly cover its surface, showing that here at least absorption is most actively going on.

In the same way the coronoid process, beneath the base of which the first, second, and third molars have successively been formed, has moved backwards by absorption cutting away its anterior, and by deposition adding to its posterior, surfaces.

The periosteum covering the back of the jaw is also active in forming the angle and the parts thereabouts.

It is worth while to add that the direction of growth in young jaws is marked by a series of minute ridges. In like manner the characteristic marks of absorption are to be found about the neck of the condyle, and the front of the coronoid process, and those of active addition about the posterior border, so that the above statements rest upon a basis of observation, and are not merely theoretical. Two cases of arrested development of the jaw (^{4}) lend a species of experimental proof to the theory of the formation and growth of the jaw above given.

There are authors, however, who maintain that the growth of the jaws is not merely a backward elongation of the cornua, together with additions to the external surface, but that an "interstitial growth" takes place.

Wedl inclines to this latter view, and the question cannot, in the opinion of the author, be held to be absolutely settled. Although it is difficult to form any definite conception of interstitial growth in a tissue so dense and unyielding as bone, the doctrines promulgated in the foregoing pages have the support of *à priori* probability, there are some rather paradoxical facts to be met with in comparative odontology. Nevertheless, there can be no doubt that backward elongation, as teeth are successively added, is sufficiently near the truth in the case of human and most mammalian jaws for practical purposes.

In the museum of the Royal College of Surgeons there is a series of models of the same mouth from the age of four up to the age of twenty-one which the author carefully examined (5), with the result of fully confirming the conclusions arrived at in the foregoing pages, and he further instituted a comparison with the jaws of certain of the anthropoid apes.

In these latter the same conclusions as to the absence of growth in the region occupied by the deciduous teeth do not hold good, as during the change from the deciduous to the permanent dentitions there is a large antero-posterior elongation.

But this elongation takes place almost entirely in the extent of the intermaxillary bones and is much greater in the orang and the gorilla than in the chimpanzee; and this difference appears to correspond with, amongst other things, the date of the closure of the intermaxillary suture, which takes place much earlier in the chimpanzee than in the other two genera of anthropoid apes, and seems to bear a proportion to the extent of development of the canines.

Thus a large part of the prognathism of these apes is due to long-continued growth in the intermaxillæ, and it would be very interesting to ascertain if the prognathism of the lower races of mankind is also due to the obliteration of the suture being deferred longer than in the European races; but unfortunately the material for this investigation does not appear to exist in this country.

It remains to notice the changes in form which the ascending ramus and the angle of the jaw undergo. In the fœtus the ramus is but little out of the line of the body of the jaw, and the condyle little raised above the alveolar border. Gradually the line of development, as is indicated even in the adult jaw by the course of the inferior dental canal, takes a more upward direction; copious additions of bone are made on the posterior border and about the angle, so that in an adult the ramus ascends nearly at right angles to the body of the jaw.

In old age, concomitantly with the diminution of muscular energy, the bone about the angle wastes, so that once more the ramus appears to meet the body at an obtuse angle. But all the changes which mark an aged jaw are the simple results of a superficial and not of an interstitial absorption, corresponding with a wasting of the muscles, of the pterygoid plates of the sphenoid bone, &c.

Eruption of the Teeth.—The mechanism by which teeth, at the date of eruption, are pushed upwards into place is far from being perfectly understood. The simplest theory would appear to be that they rise up in consequence of the addition of dentine to their base; in fact, that their eruption is due to the elongation of their roots.

Various very strong objections have been brought forward, clearly proving that this cause is quite inadequate to explain all that may be observed. In the first place, teeth with very stunted roots—which may be practically said to have no roots—are often erupted. Again, a tooth may have the whole length of its roots completed, and yet remain buried in the jaw through half a lifetime, and then be erupted. Moreover, when a healthy normal tooth is being erupted, the distance travelled by its crown often greatly exceeds the amount of addition to its length which has gone on during the same period.

To turn to comparative anatomy, the tooth of a crocodile moves upwards, tooth-pulp and all, obviously impelled by something different from mere elongation. The author's researches upon the development and succession of reptilian teeth clearly show that a force quite independent of increase in their length alters the position and "erupts" successive teeth.

It has been suggested by Constant (1) that the blood pressure may be the impelling force, the pulp and tissues beneath the tooth being more rich in their vascular supply than those above it.

It seems very possible that the blood pressure, keeping up a state of general tension, may operate to push a solid body in any direction in which there is a diminished resistance, to take up, so to speak, any unoccupied place; but it is difficult to see how it could be efficient without some such concomitant action of absorption. For the movement of an erupting tooth is not always in the direction of its long axis; for instance, the developing tooth of the frog, the newt (Figs. 99 and 174), or of the crocodile takes an oblique course, by which it travels underneath the old tooth, before moving upwards into position.

But if its path be prepared by absorption of the structures in its way, then it is very possible that the blood pressure, keeping up a certain general tension, may tend to move it along a track of diminishing resistance.

Some teeth of persistent growth, *e.g.*, the lower incisors of rodents, show a movement which cannot be accounted for in this manner. For, as is indicated by the nerve going to the open base of the pulp being bent back on itself, the base of the tooth has travelled backwards for a considerable distance, although its apex is constantly moving forwards. Underwood suggests that the cause may be the same as that which moves a shark's tooth, which apparently is the movement of the soft parts in which it is imbedded. This would seem tantamount to attributing its movements to changes in the alveolo-dental periosteum, and the direction of the fibres in an erupting crocodile tooth would lend some support to this idea, which, however, by no means explains everything.

In man, towards the eighth month of childhood the bony crypts which contain the temporary teeth in the front of the mouth begin to be removed. At the back of the mouth the crypts still retain their inverted edges; indeed, further development of the crypts is still going on in this part of the mouth.

When a tooth is about to be cut, very active absorption of its bony surroundings goes on, particularly on the anterior surface, the bone behind it being still required to form part of the crypt of the developing successional tooth. But no sooner has the crown passed up through the very wide and free orifice so formed than absorption gives place to deposition, and the bone rapidly develops so as to embrace loosely the neck of the tooth.

Additions to the margin of the alveoli keep pace with the gradual elongation of the roots of the teeth ; as this is a moderately rapid process, the alveolar portion of the jaw increases in depth almost abruptly.

But it does not do so uniformly all over the mouth ; if it did the teeth could only be closed at the back of the mouth, unless the rami elongated by an equally sudden accession of new bone.

The front teeth are erupted first, and the jaw deepens first in front ; later on the back teeth come up, and the jaw is deepened posteriorly ; meanwhile the elongation of the rami has been going on slowly, but without interruption. Thus is brought about a condition of parts allowing the whole series of teeth to come into their proper mutual antagonism.

It was pointed out by Trousseau that the eruption of the teeth is not a continuous process which, once commenced, is carried on without intermission to its completion, but that it is interrupted by periods of repose. The teeth are, according to his statement, cut in groups ; the eruption of the teeth of each group being rapid, and being succeeded by a complete cessation of the process. Individual variations are numerous ; but the following may be taken as an approximation to the truth :—

The lower first incisors are erupted at an age ranging from six to nine months ; their eruption is rapid, and is completed in ten days or thereabouts ; then follows a rest of two or three months.

Next come the four upper incisors ; a rest of a few months ; the lower second incisors and the four first molars ; then a rest of four or five months.

The canines are peculiar in being the only teeth of the temporary set which come down between teeth already in position. To this, as well as to the greater length of their root (although it is not quite clear what this has to do with it), Trousseau ascribes the great length of time which their eruption occupies, it taking two or three months for its completion. According to him, children suffer more severely from constitutional disturbance during the cutting of these teeth than of any other, but the late Dr. West thought that the eruption of the first molars causes the most suffering. It may also be noted that the canines during their development lie farther from the alveolar border than do the other teeth, so that they travel a greater distance, obviously not merely from the elongation of the root, which is wholly inadequate to effect such a change in position.

The dates of the eruption of the milk teeth vary much, no two authors giving them alike; but the whole of the deciduous teeth are usually cut by the completion of the second year. Cases in which incisors have been erupted before birth are not very uncommon. At a time when the crowns of all the deciduous teeth have been fully erupted, their roots are still incomplete, and are widely open at their bases, so that it is not until between the fourth and sixth years that the temporary set of teeth can be called absolutely complete.

At the sixth year, preparatory to the appearance of any of the permanent teeth, the temporary teeth may be observed to be slightly separated from each other; they have come to occupy a more anterior position, pushed forward, it may be, by the great increase in size of the crypt of the permanent teeth behind them. The general relation of these to the temporary teeth may be gathered from the accompanying figure, in which it will be noticed that the canines lie far above and altogether out of the line of the other teeth, and that a slight degree of overlapping of the edges of the permanent central and lateral incisors exists.

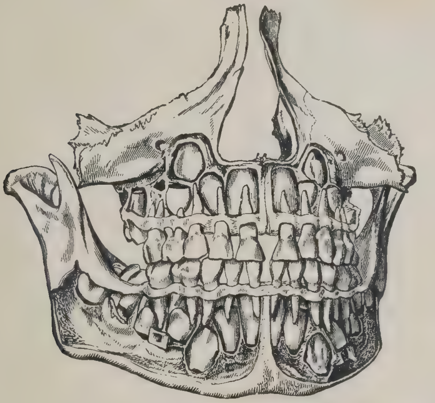

FIG. 147.—Normal well-formed jaws, from which the alveolar plate has been in great part removed, so as to expose the developing permanent teeth in their crypts in the jaw.

The premolars lie in bony cells which are embraced pretty closely by the roots of the temporary molars, and it hence happens that extraction of these latter sometimes brings them away in their entirety.

The first permanent molars are erupted in a manner closely similar to that described as occurring with the temporary teeth; that is to say, their bony crypts become widely opened out by absorption, the crown passes out, and the new bone is rapidly formed which loosely embraces the neck, prior to any considerable length of root being formed.

Last, then, follows the absorption of the root of the temporary teeth, a matter first accurately investigated by Sir John Tomes. The root, at or near to its end, becomes excavated by shallow cup-shaped depressions; these deepen, coalesce, and thus gradually the whole is removed. Although absorption usually commences on that side of the root which is nearest to the successional tooth, it by no means invariably does so; it may be, and often is, attacked on the opposite side, and in many places at once.

The cementum is usually attacked first, but eventually dentine and even enamel come to be scooped out and removed by an extension of the process. That part of the dentine, however, which immediately surrounds the pulp, appears to have more power of resistance than any other part of the tooth, and thus often persists for a time as a sort of hollow column. A live pulp is essential to the process of normal absorption, while a dead pulp is so great a barrier that dead teeth may be seen either to remain *in situ* and to deflect the permanent tooth from its course or to be themselves extruded completely by the force of the erupting successional tooth. The absorption of the temporary teeth is absolutely independent of

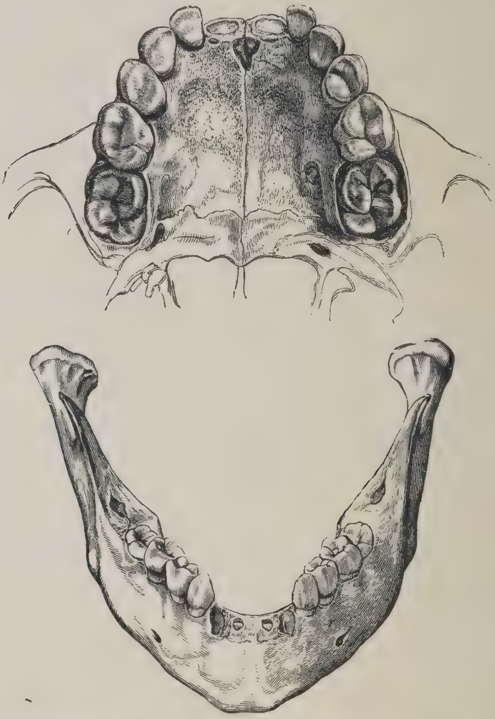

Fig. 148.—Jaws of a six-year-old child. In the upper jaw complete sockets are seen where the temporary incisors have been shed.

pressure. The varying position of the excavation has already been noticed, and it may be added that in many lower animals, for example, the frog or the crocodile, the growing tooth-sac passes bodily into the excavation made before it in the base of the preceding tooth, while if pressure had had any share in the matter the cells of its enamel-organs, &c., must have inevitably been crushed and destroyed.

Again, when the absorption and shedding of the first teeth have taken place early, before their successors are ready to appear, perfect little sockets are formed behind the lost temporary teeth (Fig. 148), cutting them off from the permanent teeth destined to follow them. Absorption, too, may attack the roots of permanent teeth, which is another reason for regarding the process as not necessarily dependent upon the approach of a displacing tooth. Closely applied to the excavation produced by absorption is a mass of very vascular soft tissue, the so-called "absorbent organ." The surface of this is composed of very large, peculiar-looking cells, bearing some little resemblance to those known as "myeloid cells," or the "giant cells" of recent authors. Microscopic examination of the excavated surface shows it to be covered with small hemispherical indentations, the "lacunæ of Howship," into each of which one of the giant cells was fitted, and in which they may sometimes be seen *in situ*.

In what manner these giant cells, or "osteoclasts," effect their work is not known, but their presence where absorption of hard tissues is going on is universal. Some suppose that they put forth amœbiform processes, others that they secrete an acid fluid, but nothing very definite is known. A curious parallel is afforded by the manner by which a fungus can drill and tunnel through and through the dentine, as may be very constantly observed in teeth long buried.

The process of absorption once commenced does not necessarily proceed without intermission, but may give place for a time to actual deposition of osseous tissue on the very surface eroded, probably by the agency of the absorbent cells themselves, which are capable of being calcified in the excavations they have individually made.

These alternations of absorption and deposition, so common a result of inflammations of the pulp or of the alveolo-dental periosteum as to be diagnostic of the former occurrence of these maladies, often occur during the normal process of the removal of the deciduous teeth, and result in the deposition of a tissue not unlike cementum in excavations made in the dentine, or even in the enamel.

The eruption of the permanent teeth is a process closely analogous to that of the temporary set. Rapid absorption of the bone, especially on the exterior surface of the crypts, takes place, and an orifice very much larger than the crown of the tooth is quickly opened out.

Hence it is that the slightest force will suffice to determine the direction assumed by the rising crown: a fragment of a root of a temporary tooth, the action of the lips and tongue, &c., are all potent agencies in modifying the arrangement of the teeth.

The temporary teeth stand vertically, the permanent teeth in front of the mouth obliquely, thus opening a space between the first incisors and the first premolar for the canine, which during development was above or below the line altogether. And, inasmuch as the crowns of the teeth are on the whole much larger than their necks, it would be manifestly impossible for them all to come down simultaneously.

The permanent teeth usually make their appearance in the following order :—First permanent molars, about the sixth to seventh year ; a little later, the lower first incisors, upper first and second incisors, the first premolars, the canines, the second premolars, the second permanent molars, the third permanent molars.

The period of eruption is variable. From a comparison of several tables, the principal discrepancies are seen to relate to the date of the appearance of the canines and the second premolars. The canine would certainly appear to belong to the eleventh and twelfth years ; but some authors consider that the second premolar is usually cut earlier, others later, than this date.

We may now revert to the phenomena observed in the alveolar processes. They were first built up as crypts with overhanging edges enclosing the temporary teeth ; then they were swept away, in great part, to allow of the eruption of the temporary teeth ; and next they were rebuilt about their necks to form their sockets.

Once more, at the fall of the deciduous teeth, the alveoli are swept away, the crypts of the permanent teeth are widely opened, and the permanent come down through the gaping orifices.

When they have done so, the bone is re-formed so as to closely embrace their necks, and this at a period when but little of the root has been completed.

Take, for example, the first upper or lower molars : their short and widely open roots occupy the whole depth of the sockets, and reach respectively nearly to the floor of the antrum and inferior dental canal. No growth, therefore, can possibly take place in these directions ; the utmost available depth has already been reached, and as the roots lengthen the sockets must be deepened by additions to their free edges.

It is impossible to insist too strongly upon this fact, that the sockets grow up with and are moulded around the teeth as the latter elongate. Teeth do not come down and take possession of sockets more or less ready made and pre-existent, but the socket is subservient to the position of the tooth ; wherever the tooth may chance to get, there its socket will be built up round it.

Upon the proper appreciation of this fact depends our whole understanding of the mechanism of teething ; the position of the teeth determines that of the sockets, and the form of the pre-existent alveolar bone has little or nothing to do with the disposition of the teeth.

Hence during the period of eruption of the permanent teeth the level of the alveolar margin is seen, in a dried skull, to be extremely irregular, the edges of the sockets corresponding to the necks of the teeth, whether they have attained to their ultimate level, or have been but just cut.

And when temporary teeth have been retained for a longer period than is natural, they sometimes become elevated to the general level of the permanent teeth (which is considerably higher than that of the temporary teeth), so that they take their share of work in mastication. When this is the case the alveoli are developed round them, and come to occupy with their tooth a higher level than before.

Enough has perhaps been said to illustrate the entire dependence of the alveoli upon the teeth, a relation of which dentists every day avail themselves in the treatment of regulation cases; it remains to say a few words as to the forces which determine the position of the teeth.

Inasmuch as when a tooth leaves its bony crypt, the bone does not at first closely embrace it, but its socket is much too large for it, a very small force is sufficient to deflect it. And, indeed, a very slight force, constantly operating, is sufficient to alter materially the position of the tooth, even when it has attained to its full length.

Along the outside of the alveolar arch the muscular lips are exercising a very symmetrical and even pressure upon the crowns of the teeth; so also the tongue, with equal symmetry, is pushing them outwards: between the two forces, the lips and the tongue, the teeth naturally become moulded into a symmetrical arch.

When the crowns of the teeth have attained such a level as to come in contact with their opposing teeth, they very speedily, from readily intelligible mechanical causes, are forced into a position of perfect correspondence and antagonism; and even at a somewhat later period than that of eruption, if this antagonism be interfered with, the teeth will often rise up so as to readjust themselves in position.

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CHAPTER VIII.

THE ATTACHMENT OF TEETH.

ALTHOUGH the various methods by which teeth are fixed in their position upon the bones which carry them pass by gradational forms into one another, so that a simple and at the same time absolutely correct classification is impossible, yet for the purposes of description four principal methods may be enumerated, namely, attachment by means of fibrous membrane, by a hinge, by anchylosis, and by implantation in bony sockets.

Attachment by means of Fibrous Membrane.—An excellent illustration of this method of attachment is afforded by the sharks and rays, in which the teeth have no direct connection with the cartilaginous, more or less calcified jaws, but are imbedded solely in the tough fibrous membrane which covers them. This, carrying with it the teeth, makes a sort of sliding progress over the curved surface of the jaw, so that the teeth once situated at the inner and lower border of the jaw, where fresh ones are constantly being developed, rotate over it, and come to occupy the topmost position (cf. description of the dentition of the sharks). That the whole fibrous gum, with its attached teeth, does really so slide over the surface of the jaw, was accidentally demonstrated by the result of an injury which had been inflicted upon the jaws of a shark.

The fibrous bands by which each individual tooth of the shark is bound down are merely portions of that same sheet of submucous membrane which furnished the dentine-papillæ. The gradual assumption of a tough fibrillated structure by that portion of the membrane which is contiguous to the base of the dentine-papilla may be traced (no such fibrous tissue being found at the base of young papillæ), very dense bands being attached to the bases of the completely calcified teeth.

A large number of fish have their teeth attached to short pedestals of bone by means of a sort of annular ligament, which allows of a slight degree of mobility. This would seem to be the case in many of those whose teeth have been generally supposed to be anchylosed, such as the *Sargus* (Fig. 128) and perhaps the eel (Fig. 153), although in the completed tooth the joint is so close that mere inspection of the developing tooth gives a hint as to the true nature of the attachment.

By the limitation of this ligament to one side, where it is greatly strengthened, we pass by easy transitions to those more specialised arrangements characteristic of hinged teeth.

Attachment by an Elastic Hinge.—The possession of movable teeth, able to yield to pressure, and subsequently to resume the upright position, was formerly supposed to be confined to *Lophius* (the angler-fish) and its immediate allies. The author has, however, found hinges in the common pike (*Esox*), and in some of the *Gadidæ* (cod tribe), as well as in certain other predatory fish ; so that, as they occur in these fish so widely removed from one another in other respects, it is probable that further investigation will bring, and, indeed, is bringing, to light many other examples of this very peculiar method of attachment, eminently suited to, and hitherto only discovered in, fish of predatory habits.

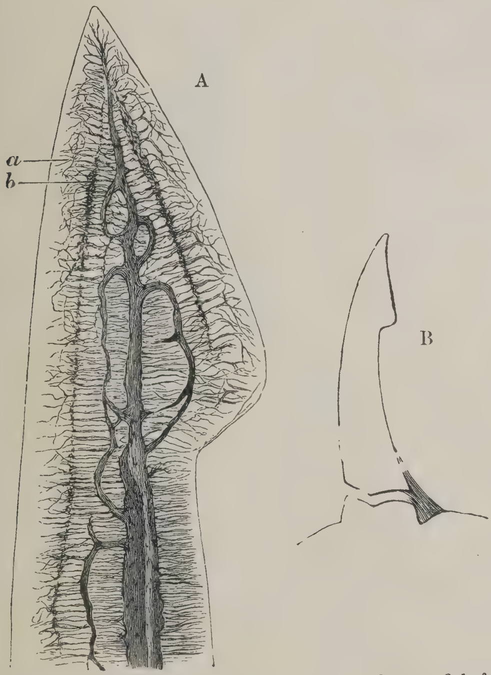

Fig. 149.—Hinged tooth of *Odontostomus*, a predatory fish from great depths. *a*. Enamel penetrated by dentinal tubes. *b*. Dentine.

In the angler-fish, which obtains its food by lying in ambush on the bottom, to which it is closely assimilated in colour, many of the largest teeth are so hinged that they readily allow an object to pass into the mouth, but, rebounding again, oppose its egress. These teeth are held in position by dense fibrous ligaments radiating from the inner side of their bases on to the subjacent bone, while the fronts of the bases of the teeth are free and, when the teeth are pressed towards the throat, rise away from the bone. The elasticity of the ligament is such that when it has been compressed by the tooth bending over towards it, it returns the tooth instantly into position with a snap. Many of the teeth of the angler are, like most fishes' teeth, anchylosed firmly.

Amongst the very peculiar predatory fish which were obtained by the *Challenger* from great depths, and which have been described by Dr. Günther, through whose kindness the author has had the opportunity of examining them, are several which possess hinged teeth. Thus in *Bathysaurus ferox*, which has a crocodile-like snout, the teeth are of no very great size, but they are attached by ligamentous hinges which allow of their being bent backwards and inwards. The teeth are not perched upon any definite pedestals, so that the motion is not very exactly limited to one plane. But in *Odontostomus hyalinus* there are some more highly specialised hinged teeth, which are laterally compressed, and have a sort of barbed point which recalls the form of some primitive bone fish-hooks. The vomer carries two such teeth of great length, behind which come some smaller ones. They are perched upon little bony pedestals of such form that, the attachment being made by means of an elastic ligament on one

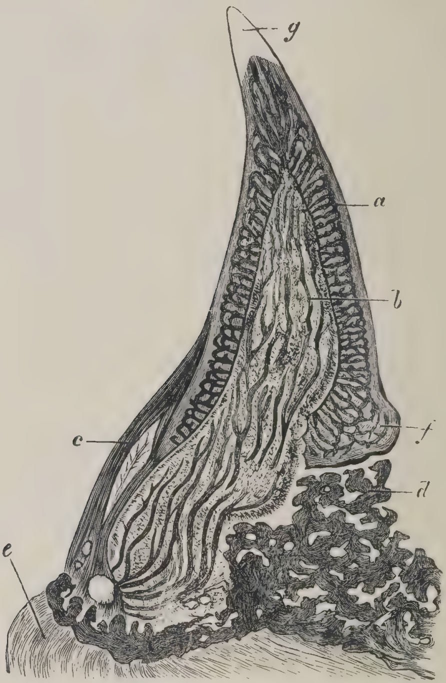

FIG. 150.—Hinged tooth of hake (*Merlucius*). *a.* Vaso-dentine. *b.* Pulp. *c.* Elastic hinge. *d.* Buttress of bone to receive *f*, formed out of bone of attachment. *e.* Bone of jaw. *f.* Thickened base of tooth. *g.* Enamel tip.

side, the motion permitted to the tooth is strictly confined to one plane.

The hake (*Merlucius*, one of the *Gadidæ*) possesses two rows of teeth, the outer and shorter of which are anchylosed, while the inner and longer are hinged.

In some respects these hinged teeth are more highly specialised than those of the angler, which they resemble in being attached by an elastic hinge on their inner sides, the elasticity of which is brought into play by its being compressed, or, at all events, bent over upon itself.

The hinge in the hake is peculiar in structure, and does not, as in the angler, consist of fibrous tissue. On the inner side of the tooth the formation of what is apparently dentine matrix goes on so that a thin edge is continued right down to the bone, which it joins just as though the tooth were going to be anchylosed there. But though matrix is formed, it is not calcified, and so the tooth is united to the bone on the side by a thin piece of flexible matrix. When seen in section this is found to be divided in the middle by a space which stops short of reaching either the top or the bottom of the flexible portion, and in this space are seen sharply bordered fibres which resemble elastic tissue in appearance. Possibly this space and its contents serve to increase the elasticity of the hinge. Of course in a decalcified section this portion looks and stains exactly like the rest of the matrix which was calcified, except that it does not contain vascular canals. These, however, are continued down to a lower level on the inside than on the outside of the space, and probably calcification also had advanced to a lower level here, as a dried tooth ends in a thin edge in this situation.

The pulp is highly vascular, and its vessels are so arranged that by entering the pulp through a hole in the flexible portion, which is near the axis of motion, they escape being stretched or torn during the movements of the tooth. The free edge of the base of the tooth itself is modified so as to be particularly fitted for resisting the jars to which a movable tooth must at times be exposed, and so also is the pedestal of bone upon which it strikes.

As is seen in the figure, the base of the tooth on the side opposite to the hinge is thickened and rounded. The advantages which such a form must possess over a thin edge when striking against the bone are sufficiently obvious. This thickened edge is received upon a little buttress of bone, and it occupies a much higher level than the opposite thin edge to which the hinge is attached, so that the tooth cannot possibly be bent outwards without actual rupture of the ligament.

And what is not a little remarkable is that, whilst the hake, the most predatory of all the *Gadidæ*, is possessed of these very perfectly hinged teeth, other members of the family have teeth movable in a less degree, and others again have teeth rigidly fixed. Indeed, the hake itself has its outer row of teeth anchylosed. So that within the limits of a single family we have several steps in a gradual progression towards a very highly specialised organ.

In the hinged teeth already alluded to the purpose served by their mobility seems to be the catching of active fish, and the elasticity resides solely in the hinges; but the common pike possesses many hinged teeth which seem to be more concerned in the swallowing of the prey after it has been caught, and there is no elasticity in the hinges, the resilience of the teeth being provided for in another way.

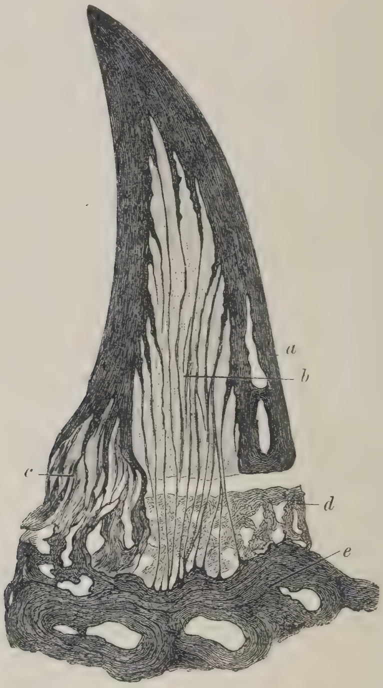

Fig. 151.—Hinged tooth of pike. *a*. Dentine. *b*. Elastic rods formed of uncalcified trabeculæ which might have become bone. *c*. Hinge, not itself elastic. *d*. Bone of attachment. *e*. Bone of body of jaw.

The teeth which surround the margins of the jaws are anchylosed, and they are more or less solidly filled up in their interior with a development of osteo-dentine, which, by becoming continuous with the subjacent bone, cements them to it. The manner of development of this is by rods of calcifying material shooting down through the central pulp (see p. 194). In the hinged teeth also these trabeculæ shoot downwards and become continuous with the subjacent bone, but instead of rigidly ossifying they remain soft and elastic, so that the tooth is like an extinguisher fastened down by a large number of elastic strings attached to different points on its interior, and hinged at one side.

The elasticity is very perfect. The teeth depressed and suddenly released return with an audible snap. The elasticity resides solely in these strings, for if they be divided by carefully slipping a cataract needle under the tooth without injuring the hinge, the tooth will stay in any position into which it is placed.

The method in which the resilience of these teeth is utilised will be described subsequently, under the heading "The Teeth of Fishes."

Thus we have examples of hinged teeth occurring in several distinct orders of fish: in Acanthopterygii (*Lophius*), in Anacanthini (*Merlucius*), in Physostomi (*Esox*, *Bathysaurus*, *Odontostomus*), whilst, on the other hand, they are not universal even within the limits of well-defined families.

Hence it is noteworthy (i.) that hinged teeth have arisen independently in families of fish widely removed from one another, and (ii.) that, whilst the general object of mobility and elastic resiliency is attained in all, it is by different mechanisms, and apparently by the least modification possible of the existing fixed teeth of the family.

Attachment by Anchylosis.—In both the socketed and the membranous methods of attachment, an organised, more or less vascular, membrane intervenes between the tooth and the jaw-bone. In the mode of attachment now under consideration there is no such intervening membrane, but the calcified tooth substance and the bone are in actual continuity, so that it is often difficult to discern with the naked eye the line of junction.

The teeth may be only slightly held, so that they break off under the application of but a moderate degree of force, or they may be so intimately bound to the bone that a portion of the latter will usually be torn away with the tooth.

A very perfect example of attachment by anchylosis is afforded by the fixed teeth of the pike, of which the central core is composed of osteo-dentine. The method by which the entire fusion of this tissue with the bone beneath it takes place has already been alluded to, the similarity of its method of calcification with that of bone rendering the fusion easy and complete.

From the accounts which pass current in most books it would be supposed that the process of attachment by anchylosis is a very simple matter, the base of the dentine-papilla or the dental capsule by its calcification cementing the tooth on to a surface of the jaw-bone already formed. In a few animals (examined), however, the author has found that this conception does not at all adequately represent what really takes place. It seldom, perhaps never, happens that a tooth is attached directly to a plane surface of the jaw which has been formed previously. The union takes place through the medium of a portion of bone (which may be large or small in amount) specially developed to give attachment to that one particular tooth, and after the fall of that tooth is itself removed.

For this bone the author proposed the name of "bone of attachment," and it is strictly analogous to the sockets of those teeth which have sockets. It is well exemplified in the Ophidia, a description of the fixation of the teeth of which will serve to convey a good idea of its general character. If the base of one of the teeth with the subjacent jaw-bone be submitted to microscopical examination it will be found that the layer of bone which closely embraces the tooth contrasts markedly with the rest of the bone. The latter is fine in texture, its lacunæ, with their very numerous fine canaliculi, very regular, and the lamination obviously referable to the general surface of the bone. But the "bone of attachment" is very coarse in texture, full of irregular spaces very different from the regular lacunæ, and its lamination is roughly parallel with the base of the tooth. The dentine of the base of the tooth also bends inwards (Fig. 152), and its tubes are lost in the osseous tissue, a blending so intimate resulting that in grinding down sections the tooth and the bone of attachment often come away together, the tooth and this bone being more intimately united than this special bone is with that of the rest of the jaw.

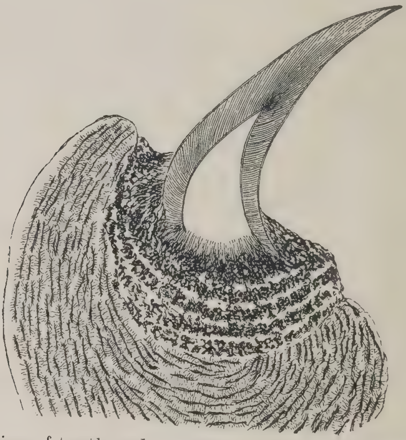

Fig. 152.—Section of tooth and a portion of the jaw of a python, showing the marked difference in character between the bone of attachment and the rest of the bone.

A study of its development also proves that it has an intimate relation with the tooth with which it is continuous, for it is wholly removed with the fall of the tooth, and is again formed for the next tooth which comes into position. The periosteum of the rest of the jaw-bone appears to take an important share in the formation of this special bone substance, and the tooth capsule, by its ossification, apparently contributes little.

Hertwig has thrown out the suggestion that parts of the tooth sockets and of the basal plates met with in fish and reptiles represent the cementum, and that it may even be that the bones surrounding the mouth have originated from the coalescence of such plates ; but this view does not commend itself to the author.

In the frog the teeth are commonly described as being attached by their bases and outer surfaces to a continuous groove, of which the external wall is the higher. Such is, however, an inadequate description of the condition, the tooth as seen in section being attached on its outer side by a new development of bone, which extends for a short distance up over its external surface. For the support of its inner wall there springs up from the subjacent bone an osseous pillar, which is entirely removed when that tooth falls, a new pillar being developed for the next tooth.

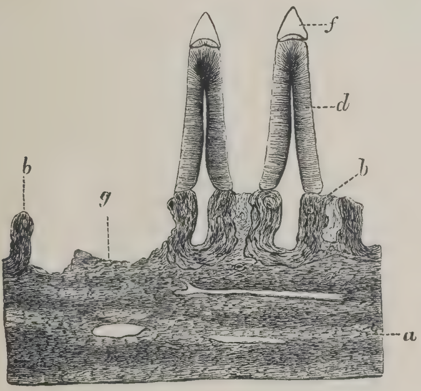

Fig. 153.—From lower jaw of an eel. *a*. Bone of jaw. *b*. Bone of attachment. *d*. Dentine. *f*. Enamel. *g*. Space vacated by a shed tooth.

When the teeth are, as in many fish, implanted upon what to the naked eye appears to be nothing more than a plane surface of bone, a microscopical examination generally, in fact in all specimens examined by the author, reveals either that the individual teeth are implanted in depressions much larger than themselves, the excess of space being occupied by new and specially formed bone, or else that the teeth surmount pedicles which are closely set together, the interspaces being occupied with a less regular calcified structure.

A good example of the latter method is afforded by the eel (Fig. 153), in which each tooth surmounts a short hollow cylinder of bone, the lamination, &c., of which differs markedly from that of the body of the jaw-bone. When the tooth which it carries is shed, the bone of attachment, in this case a hollow cylinder, is removed right down to the level of the main bone of the jaw, as is well seen in the figure to the left of the teeth in position. Under a higher magnifying power the bone at this point would be found to be excavated by

"Howship's lacunæ." As an anchylosis, the implantation of the teeth is less perfect than that of the teeth of the snake, for the dentinal tubes at the base of the tooth are not deflected and do not in any sense blend with the bone beneath them. Accordingly, the teeth are far less firmly attached, and break off quite readily. Indeed, the actual attachment may perhaps be of a fibrous nature, although a bone of attachment pedestal is formed.

Another instance of the formation of a kind of pedestal, which in this instance is sunk within the substance of the surrounding bone, is found in *Sargus* (Fig. 127). Here the attachment of the working tooth to the subjacent portion is by means of fibrous tissue (Fig. 129), though the submerged portion appears in this case to be made by the tooth pulp itself.

A transition towards a socketed type of implantation is seen in some of the cod family. Thus in the haddock the teeth surmount a hollow cylindrical "bone of attachment," resembling in many particulars those of the eel. The teeth do not, however, simply surmount the bony cylinders, but are continued for a short distance within them, definite shoulders being formed which rest on the rims of the cylinder. The base of the tooth does not, however, contract or taper any more, and is widely open, so that it cannot be considered that any close approximation to a root is made. The pulp cavity of the tooth becomes continuous with the cavity of the osseous cylinder, into which the pulp is for a short distance continued. Not only is the pulp continued down, but its odontoblast layer is here traceable, and this relation of parts recalls that seen in *Sargus* (cf. Fig. 128, p. 193).

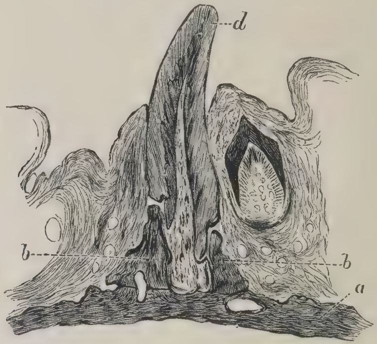

Fig. 154.—From lower jaw of a haddock. *a*. Bone of jaw. *b*. Bone of attachment. *d*. Dentine of tooth.

The bony supports of the teeth originate in many osseous trabeculæ which spring up simultaneously from the bone of the jaw beneath the new tooth; these coalesce to form a net-like skeleton, which rapidly becomes filled in by the progress of ossification. So far as the author's researches enable him to conclude, there is this much in common in all forms of attachment by anchylosis, that, no matter how different the naked eye results of the process may be, the tooth as it comes into position is secured by an exceedingly rapid development of bone, more or less directly an outgrowth from the jaw-bone itself, and which is in some unseen manner stimulated into activity by the proximity of the tooth.

The teeth of the mackerel present an interesting variety of attachment by anchylosis. The margins of the jaws are very thin, and by no means fleshy, and in them there is a deep groove between the outer and inner plates of the bone. In this groove the teeth are attached, their sharp points projecting beyond the edges of the bone, and they are held in their places by a network or scaffolding of "bone of attachment" which is developed between their sides and the inner surface of the bone. They are, so to speak, hung up in their place, and their open bases rest on nothing, or at least on nothing hard.

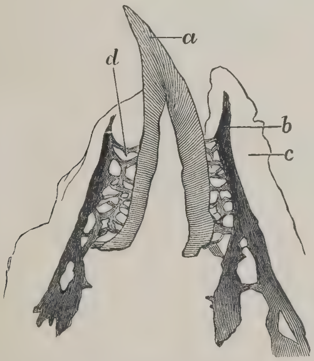

FIG. 155.—Tooth of mackerel, showing its peculiar mode of anchylosis. *a*. Tooth. *b*. Bone of jaw. *c*. Gums. *d*. Bone of attachment.

Attachment by Implantation in a Socket.—In this, as in anchylosis, there is a special development of bone which is modelled to the base of the tooth, but, instead of its being in actual close continuity with the dental tissues, there intervenes a vascular organised membrane in great part, at all events, derived from the tooth-sac. The manner in which the sockets are, so to speak, plastered around the roots of the teeth and are perfectly subservient to and dependent on them, has already been described. Little, therefore, need be added here, save that the soft tissue intervening between the bone and the tooth is not separable, either anatomically or developmentally, into any two layers, but is a single membrane termed the "alveolo-dental periosteum." That it is single when completed is a matter of absolute certainty; there is no difficulty in demonstrating it *in situ*, with vessels and bundles of fibres traversing its whole thickness, from the tooth to the bone, or *vice versâ*.

The nature and development of the sockets in those few reptiles and fishes which have socketed teeth require further examination. From what has been seen in sections of the jaws of a young crocodile, the author is inclined to regard them as in all respects similar to the alveoli of mammalian teeth. At all events, they are not developed in that same subserviency to each individual tooth; on the contrary, successive teeth come up and occupy a socket which is more or less already in existence.

Although there are animals in which implantation in a spurious socket is supplemented by anchylosis to the wall or to the bottom of the socket, few examples of anchylosis occurring between the tooth and the bone of the socket have ever been met with in man, or indeed in any mammal exemplifying a typical socketed implantation of the teeth.

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PART II.

CHAPTER IX.

GENERAL INTRODUCTORY REMARKS.

Before proceeding to the description of the teeth of Fishes, Reptiles, Mammals, of which it is only possible to give the barest outline, it seems desirable, at the risk of some recapitulation, to devote a few pages to those general principles which underlie and render interesting and intelligible the details with which we shall be concerned.

Before the day of Darwin it was customary to explain those resemblances and points of identity which the study of comparative anatomy and of development revealed upon the supposition that there was some sort of type or standard organisation and that all others were arrived at by modifications and departures from this type, such modifications being introduced with a direct purpose in view, in order to fit the creature to a special habit of life.

This "type" theory suggested a clue to the explanation for the possession by an animal of some *highly specialised* organ which detailed comparative study reveals as but the homologue of some simpler structure present in allied animals, and likewise to the reduction or suppression of an organ in one animal which is of ordinary size and functional activity in its congeners.

This is as true of teeth as of any other organ; indeed, they afford many admirable examples.

Thus the tusks of the boar or of the *Sus babirussa* (figured on p. 458), large and peculiar though they be, are not new developments, but are merely the canine teeth which all pigs possess, and which in this species attain to unusual dimensions. In the same way the enormous straight tusk of the male narwal is nothing more than an incisor tooth of one side, the fellow to which has been checked in its development; but this latter is not missing, for it remains throughout the life of the animal buried within its socket. In the female narwal both of the teeth, being rudimentary, are permanently enclosed within the sockets, and are, of course, not of the smallest service to the animal, directly or indirectly. Furthermore, as has been shown by the late Professor Sir W. Turner, in young specimens, a second pair of vestigial incisors are to be found which in the adults have disappeared.

The modern school of morphologists, rejecting the "archetype" theory, refer these correspondences detected between dentitions upon the whole dissimilar to one another to a more intelligible cause, namely, inheritance. Assuming, as every evidence compels us to assume, that the many divergent forms which we observe have been derived by progressive modifications and differentiations from fewer and simpler ancestral forms, we shall have no difficulty in seeing how, by such processes as are well known to occur, namely, the dwindling of disused organs and the exaggerated development of those which are of considerable use, great differences may ultimately result.

To illustrate what is meant by this so-called "adaptive modification," this suppression of things that are not needed, and increased development of those most used, we may allude to the dentitions of non-venomous and venomous snakes (p. 287).

In them we see that the typical dentition in the snake, as exemplified by the pythons, consisted of three complete rows of teeth, two in the upper jaw, one of which occupied the maxilla, and one in the lower. Then in the colubrine *Opisthoglypha* some of the maxillary teeth become enlarged and grooved, while the snakes are only doubtfully poisonous; then, further, in the *Proteroglypha* the front teeth of the maxilla become grooved and enlarged to form the poison fang, the complete row of maxillary teeth becoming reduced to a few small teeth behind it, the maxilla itself undergoing reduction in an antero-posterior direction.

Finally, in the vipers the poison fang is enormously developed, the rest of the maxillary teeth are lost, and the maxilla so shortened as to be almost square, and coincidently acquiring the power of movement of rotation through a wide angle, so as to lay the poison fang down flat when not in use. This mobility of the maxilla was foreshadowed in the cobra, in which the bone is but slightly movable. The same serial modification is to be observed in the poison fangs themselves (p. 291), which range from the very complete canal of the vipers, traversing the whole length of the fang and terminating in an orifice at the apex through the closure of the laterally placed groove in the cobra, and the open grooves of some of the other *Proteroglypha*, to the grooveless teeth of the non-poisonous snakes.

Thus there can be found amongst living snakes a most complete chain of transitional forms of poison apparatus.

But in many poisonous colubrine snakes the three or four small and useless teeth lingering upon the maxillary bone, though their function has gone, serve to indicate to us in some measure the gradual process by which that singularly perfect adaptation of means to an end, the poison apparatus of the viper, has been attained.

Good examples of rudimentary teeth are to be found in the larval teeth of the edentulous sturgeon, or of the whalebone whales, or in the teeth buried beneath the horny plates of the deflected portion of the dugong's jaw, all of these being of absolutely no service to their possessors. Some teeth have disappeared utterly; thus the upper incisors of Ruminants are gone, and no rudiments have been detected at any stage; others still remain in a stunted and dwindled form, and do not persist throughout the lifetime of the animal, as, for instance, the first premolars of the horse, or two out of the four premolars of most bears.

The teeth of *Ornithorhynchus* do work for their possessor till the animal approaches its adult size; they are then curiously supplanted by a horny development of the gums.

Darwin believed that any modification in the structure of a plant or an animal, which is of benefit to its possessor, is capable, nay, is sure, of being transmitted and intensified in successive generations, until great and material differences have more or less masked the resemblance to the parent form.

Just as man, by picking out and breeding from those modifications of form, &c., that please him best, has been able, in the course of a few years—in a length of time altogether infinitesimal as compared with the time during which the surface of land and sea has been nearly in its present form, to say nothing of the enormously longer earlier geological epochs—to profoundly modify the breeds of dogs, of horses, of pigeons and of numbers of plants, all of which are known to have had a common origin, so in nature forces are and ever have been in perpetual operation effecting the same result.

A pigeon-fancier desires a pigeon of particular plumage, with some feathers differing slightly from any pigeon he has ever seen or heard of *; he knows by experience that little variations are for ever arising, and that by watching a sufficient number of young ones, and rigorously picking out those which at all tend in the direction required, he will get what he requires, and will even state with confidence that in so many years he will make a breed with the peculiarity desired. And exactly as the required plumage is obtained, so in nature the tooth that is "wanted," *i.e.*, the dentition that is excellently well adapted to do its work, may have been elaborated by the operation of that law known as "survival of the fittest."

The number of animals born or of seeds germinating is vastly in excess of the capabilities of the area in which they live to support them, so that a weeding-out process, the death of a large number, is a necessity. And those are the most likely to die or to fail to breed which are, in any way, placed at a disadvantage.

It is, therefore, quite enough that one of the small variations for ever arising in animals shall be of advantage for us to see how the peculiarity is likely to be transmitted and intensified in successive generations without the intervention of man, which we know can effect such a result.

The question has been well presented by Wallace, who points out that we must not think so much of variations in individuals as in groups of individuals; for instance, it is a familiar fact that people vary in height, so that any hundred persons may be divided into fifty taller and fifty shorter persons. Now if a little extra height were of advantage, many or most of the fifty would be placed under circumstances to experience it, though some might not. In the same way, if we grouped one hundred animals whose teeth varied a little in respect of strength into the fifty weaker and fifty stronger, it is easy to see that the stronger fifty would get the better of the others in the struggle for existence on the whole, would be more certain to propagate their kind, and would repeat in a majority of their progeny those peculiarities which had helped themselves to survive.

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* An eminent pigeon-fancier, Sir J. Sebright, told Mr. Darwin that he could produce any given feather in three years.

Thus the doctrine of natural selection, or survival of the fittest, is as fully applicable to the teeth of an animal as to any part of its organisation, and the operation of this natural law will be constantly tending to produce advantageous or "adaptive" differences. On the other hand, the strong power of inheritance is tending to preserve even that which, in the altering conditions of life, has become of little use, and thus we may understand vestigial teeth to be those which are in process of disappearance, having ceased to be useful to their possessors, but which have still for a long time lingered upon the scene. And it must be remembered that, just as natural selection brings an organ up to its fullest standard of efficiency, so the cessation of selection will tend to allow its variations in a downward direction to establish themselves. In other words, the continuance of that selection which elaborated an organ is required to maintain it at that standard.

For the efficient action of natural selection, it will be seen that two conditions are essential: the one a competition amongst the organisms concerned, and the other a tendency to vary, the variations being capable of being inherited.

Now, however produced, it is a familiar fact that variations occur, and that they are capable of perpetuation, as every florist or breeder of animals knows.

It was formerly supposed that the variations seized upon by natural selection and intensified in successive generations were of necessity small, so small that it was difficult to see how their advantage would really be felt.

But since attention has been drawn to this subject, and careful measurements and weighings have been taken of large numbers of wild specimens of the same species, it has been found that the variations are often far from being insignificant in extent.

Then Wallace (7) points out that the variation in common species often reaches 20 per cent. of the size of the part implicated, and this without reference to the general size of the animal. The jaws of the wolf may be taken as an example; in ten specimens variation to the extent of an inch and a half in length occurred. If there be an advantage in it, it is easy to see how in a few generations a very distinct advance in the direction of increased length or shortness of jaw might be established.

The same species will be found to vary in size according to the locality whence it has come. Thus a species having a large range in latitude will generally be found larger in its northern than in its southern areas.

Variability in the number of teeth is much more common than has generally been supposed. Thus Bateson (¹) found supernumerary teeth in 8 per cent. of the jaws of gorillas, orangs, and chimpanzees which he examined. In *Phocidæ* supernumerary teeth were present in 7 per cent. of the specimens examined, in 4 per cent. of *Otariidæ*, in 3 per cent. of wild and in 8 per cent. of domestic *Canidæ*, in less than 2 per cent. of wild, but in 9 per cent. of domestic, *Felidæ*.

Before leaving this section of the subject, an instructive illustration of the operation of these agencies may be given.

It is easy to understand how a "rodent" type of dentition may be beneficial to its possessor by rendering accessible articles of food wholly unavailable for creatures which have no means of gnawing through a shell or other hard body. Now it happens that in three regions of the world, more or less completely cut off from one another, three animals, in parentage widely dissimilar, have arrived at dentitions of "functionally rodent" type.

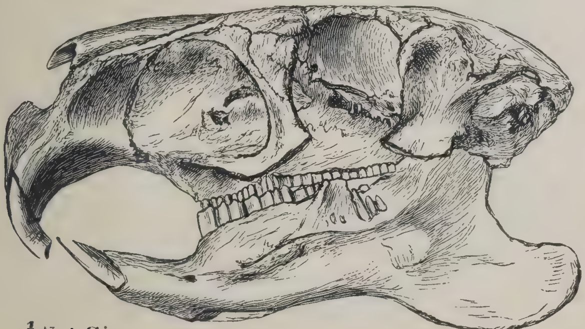

FIG. 156.—Skull of a placental rodent (*Capybara*), showing general character of a rodent's dentition.

Thus in Australia, a region practically wholly monopolised by marsupials, a marsupial, the wombat, has a dentition very much like an ordinary placental rodent. In the island of Madagascar, one of the very few parts of the globe without indigenous rodents (except a few *Muridæ*), a lemurine animal, the *Cheiromys*, has a dentition modified in a similar direction (though it is probably employed to obtain a different sort of food); and elsewhere, scattered all over the world, we have the ordinary rodents.

In fact, three sets of creatures, as widely different from each other in parentage as they well could be, have been modified by natural selection until they have dentitions by no means identical but for working purposes not unlike. Such instances are examples of what is now known as "convergent evolution."

It cannot be supposed that these three creatures have arrived at their peculiarities by the way of common origin; their ancestry must have been widely different, the regions in which they live have been isolated from one another for countless years, and yet they have each got to a "practically rodent" type of dentition.

Of extinct lemurs little is known and of the ancestry of *Cheiromys* nothing; but in the compact group of marsupials, still living in Australia, we are able to dimly see some of the progressive steps which seem to tend towards this rodent form of dentition. In Australia, roughly speaking, there are nothing but marsupials, in Madagascar more lemurs than anything else; and in each case, out of the material at hand, natural selection has manufactured a "rodent" dentition.

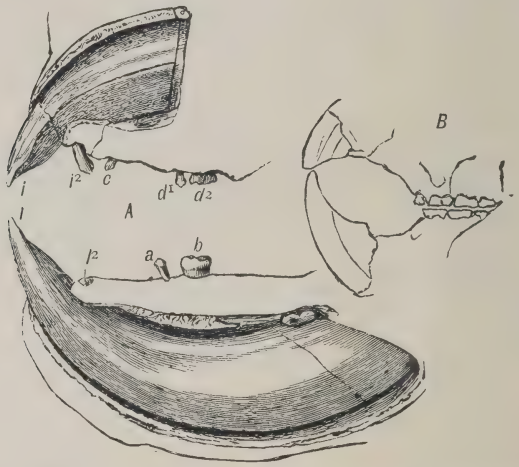

FIG. 157.—A. Milk teeth of the lemurine *Cheiromys*, with the permanent incisors just coming into place. It differs from any rodent by having many milk teeth. *i*. Permanent incisor. *i* 2. Deciduous incisor. *c*. Deciduous canine. *d*, *d* 2. Deciduous molars. *l*. Lower permanent incisor. *l* 2. Lower deciduous canine. *d a*, *d b*. Lower deciduous molars. B. Reduced outline figure of its permanent dentition, in which it closely mimics the true rodents.

At the same time the force of inheritance is seen in each of them retaining characteristics of the groups whence they have been derived, so that underlying the *primâ facie* resemblance in the teeth there are points in their several dentitions whereby the wombat shows its marsupial affinities, and the aye-aye its quadrumanous relationships.

The approximation to a rodent type of dentition by a number of widely different animals has led to the suggestion being made that it does not follow that all existing rodents have had a common origin. Thus Oscar Schmidt (5) writes :—" A comparison of the very different shapes of the molars in the rodents among one another, and the approximation of many genera—not as yet decided rodents—to the rodent type (for instance, the wombat, the fingered animal—aye-aye —and the rock coney), render it extremely probable that even our present rodents are not of one and the same origin. The fact remains, animals of different derivation having attained a similar exterior, succeed extremely well in the struggle for existence, or even better, in their endeavour to obtain food. Unlike as they may be in one point, they are incontestably alike, *i.e.*, in the development of continuously growing incisors."

An example of the same kind of thing is to be seen in the occurrence of hinged teeth in various families of fish (see p. 233), in which the requirements of a hinge and of a means for restoring the bent-down tooth to the upright position are attained by different mechanism according to the differences in the raw material, if such an expression may be allowed.

Examples of " convergence " are of course not confined to the teeth, but occur throughout the animal kingdom, and in many different organs of the body.

In addition to these modifications which are of direct use to the individual in the way of assisting in the procuring of food, &c., any character which would enable one male to get an advantage over other males, and so render him more certain to propagate his kind, will be sure to be transmitted and intensified.

Thus we can understand how the males of some species have become ornamented ; how the males of many birds have come to sing ; and what is of more immediate concern to us, how the males of some animals have become possessed of weapons which the females have not. The possession of weapons by the male is strikingly exemplified in the teeth of some animals. The males of many frugivorous monkeys have canine teeth much larger than those of the females ; they are cut late, coincidentally with the attainment of sexual maturity, and are useful to their possessors as weapons in their combats with other males. The male narwal has its single elongated tusk ; the male dugong has tusk-like incisors ; in the respective females these same teeth are insignificant.

But the most striking instance of the teeth being modified, so as to serve as weapons for sexual combat, is afforded by some members of the group of ruminants, amongst whom, as Cuvier long ago pointed out, those which are armed with horns have no canine teeth, and *vice versâ*—a generalisation which, although subject to slight exceptions, remains upon the whole true.

The male musk-deer (*Moschus moschiferus*) has canine teeth of enormous length, while it is quite without horns ; the female has canine teeth so reduced as to be functionless. The male muntjak, which has very short horns, has canine teeth, but of much smaller size than those of the musk-deer. Other examples of hornless deer furnished with canine teeth are to be found in Swinhoe's water-deer (*Hydropotes inermis*) and in the *Elaphodus cephalophus* (which has very small antlers), a Chinese deer more recently discovered, and in the *Tragulidæ*. It is obvious that males furnished with weapons more powerful than their fellows will be more likely to prove victorious in their battles, to drive away the other males, to monopolise the herd of females, and so to transmit their own peculiarities to offspring, which will again be favoured in the same way. Thus it is easy to see how, amongst gregarious animals, the development of teeth serving as sexual weapons is likely to be favoured, generation after generation, until canines as highly specialised as those of the musk-deer, or the wild boar, are attained.

It will suffice to indicate to the reader that he must be prepared to find that the teeth are profoundly susceptible of modification, but that, amid all their varied forms, the evidences of descent from ancestors whose teeth departed less from the typical mammalian dentition are clearly traceable in the existence of vestigial teeth and other such characters. And, although it is by no means probable that more than a part of the agencies which are at work have been recognised, natural selection and sexual selection appear to be competent to produce most of the phenomena of modification observed.

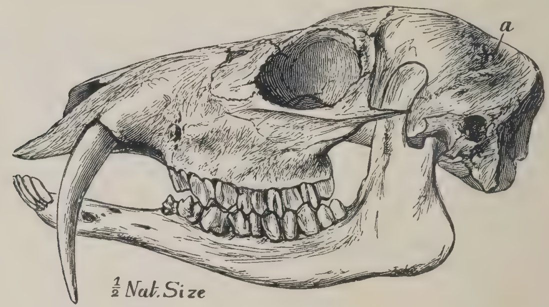

FIG. 158.—Cranium of *Moschus* (male), showing the long canine tooth.

There remains one other influence, much more obscure in its nature, to be touched upon, namely, "correlation of growth" or "concomitant variation." When we find that when horns are developed canine teeth are absent, or that, after a boar has been castrated, his tusks cease to grow, although we may be quite unable to conceive the precise manner in which the one thing influences the other, we can see that there is a consistency in the development of the sexual weapon ceasing coincidently with the destruction of the sexual apparatus, or in the fact that two kinds of weapon are not developed in the same animal.

But there are some correlations of growth of a still more recondite nature, in which the connection is less obvious. Of this kind is the relation which exists between peculiarities of the skin and of the teeth: the Edentata, abnormal in their skins, are different from most other Mammalia in their teeth; whales, yet more aberrant in the nature of their skins, have only rudimentary teeth, in place of which, after birth, plates of whalebone are found.

Darwin (³) has collected a number of curious instances of relations existing between hair and teeth. In general terms it may be said that any great abnormality in the hair goes hand in hand with an abnormality of the teeth. Thus there is a breed of dogs found in Turkey which is almost hairless, and which has very few teeth, the dentition being reduced to a single molar on each side, together with a few imperfect incisors *; in the human subject inherited baldness has been often found to be associated with inherited deficiency of the teeth; on the other hand, redundance of hair has in several cases been accompanied by absence of teeth.

In the case of the now famous hairy family of Burmah, the peculiarity of silky hair being developed over the face was transmitted to a third generation, and in each case the teeth were very deficient in number. A number of years ago a hairy man and his son, said to have come from the interior of Russia, were exhibited in London, and they were almost toothless.†

A good many years ago a hairy woman (Julia Pastrana) was exhibited in London, of whom it has commonly been reported that she had an excessive number of teeth. Certain it is that her mouth was very prominent, and that she was described as "dog-faced" and "pig-faced," but models have been presented to the Odontological Society by Mr. Hepburn which are indisputably known to be models of her mouth, and these do not show any excessive number of teeth. The teeth, at least such of them as can be seen, are enormously large, but the mouth is affected with general hypertrophy of the gums and alveolar processes to such a degree that only a few of the teeth can be made out.

But this does not make her case the less interesting to the odontologist, for in the huge teeth, the enormous papillæ of the gum, and the redundant hairs on the face, we have evidence of a disposition to hypertrophies of the integument affecting in different places the different tegumentary appendages which happen to be there. And that the teeth are dermal appendages has been shown at a previous page (see p. 3). But we must not go further than to say that great abnormality of hair goes hand in hand with abnormality of teeth.

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* The author has described an example of great reduction of the teeth in an individual specimen of the very hairy monkey *Colobus caudatus* (⁶).

† The man's mouth exemplified the dependence of the growth of the jaw upon the presence of teeth. Ordinarily the increase in size between childhood and adult age takes place by a backward elongation, which allows for the successive development and eruption of the molars behind the spaces occupied by the temporary teeth. But this man never had any true molars, and no such backward elongation of the jaw had ever taken place, so that, though he was a full-sized man, his jaw was no larger than a child's.

On the other hand, redundance of hair has in several cases been accompanied by absence of teeth.

He would indeed be a rash man who ventured to assert that he had recognised all the agencies which are at work in the modelling of animal and vegetable forms; but it is safe to say that, at the present time, we are acquainted with "natural selection," or "survival of the fittest," an agency by which variations beneficial to their possessors will be preserved and intensified in successive generations; with "sexual selection," which operates principally by enabling those possessed of certain characters to propagate their race, while others less favoured do not get the opportunity of so doing; and with "concomitant variation" between different parts of the body, an agency much more recondite in its operations, but by which agencies affecting one part may secondarily bring about alterations in some other part.

And operating in the contrary direction, we have a certain fixity of organisation, so that the power of inheritance is constantly asserting itself by the retention, for a time at all events, of parts which have become useless, and by the occasional reappearance of characters which have been lost (atavism).

With regard to the direct action of environment upon the teeth of the individual or upon the race within a comparatively few generations, some rather contradictory statements have been made as to the effect of high feeding, improvement of breed, etc., upon the cutting of the teeth, early maturity being of course one of the aims of the improvers of farm stock.

With regard to horses, neither high feeding nor improved breed seems to have made any difference, *e.g.*, a Highland pony at five years has as full a mouth as the most pampered horse. But in cows it seems to be different. Thus Highland cattle have all the permanent teeth at four and a half or five years of age, whereas some improved breeds have a full mouth at three years (Williams (8)).

Prof. Brown (2) has been unable to trace any change in thirty years, though, if the older writers were accurate, a real acceleration has taken place over much longer periods. He, however, quite denies that high feeding, of a litter of pigs for example, will produce any immediate effect, and strongly lays down that their dentition is a reliable test of age. [That insufficiency of certain constituents of the food may have an injurious effect on the development of teeth has been shown by Mrs. M. Mellanby (4). There is also evidence to support the view that some of the endocrine organs, particularly the thyroid, exert an influence on the development and regularity of the teeth.]

From what has been said, the reader will have gathered that, in order that evolution may go on, it is necessary, firstly, that animals shall vary, and, secondly, that these variations shall be inherited; granted these two propositions, the process is intelligible.

That animals do vary we have already seen, but various views are current as to the causes of that variation.

One school, supported by the very numerous measurements of prawns taken by the late Prof. Weldon (prawns were selected as being creatures of which it was easy to procure large numbers), holds that the variations are, so to speak, fortuitous; that is to say that they take place round a mean, in the same proportions as would result were they determined by the tossing up of a coin, those which are advantageous getting preserved by selection, while those which are not die out.

The other school hold that they are by no means fortuitous, but that they take place along certain defined lines towards which there is an ever-acting tendency, and that the force in operation is that of the environment and habits of the animal.

This involves another consideration, namely, whether characters acquired by an animal in its lifetime can be and are transmitted to its progeny. And on this point also naturalists are divided into two camps: those who hold that the agencies enumerated are all-sufficient, and, with Weissman, hold that qualities acquired by the individual during its lifetime under the influence of outside conditions can never be transmitted; and those, the so-called Neo-Lamarckians, who believe that they can.

Amongst the strongest advocates of this latter view are several of the American naturalists who have given much attention to teeth, and base their arguments largely upon them, especially Profs. Cope, Ryder, and Osborn, to whose views we shall have from time to time to recur.

But as their arguments relate chiefly to what has been observed with regard to mammalian teeth, it may be more convenient to defer their consideration for the present.

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CHAPTER X.

THE TEETH OF FISHES.

In the following pages the limits of space forbid more than a brief account of a few typical forms. In the class of fish the task of selection of forms for description is no easy one; for the almost infinite diversity of dentition which exists in it makes it a matter of peculiar difficulty to frame any general account, or to do more than present before the reader a description of a few individual types from which he may gather, as best he can, a general idea of piscine dentition.

The modern classification * of the class Pisces separates off a subclass Agnatha, which is without paired fins and without a lower jaw. It comprises

The Cyclostomata (*vel* Marsipobranchii), which embrace the lampreys and myxinoid fishes, as well as some extinct forms.

Pisces.—Aquatic, cold-blooded animals breathing by means of internal gills. More or less covered with scales and with appendages in the form of fins.

I. Elasmobranchii.—Mouth ventral. Body covered with dermal denticles. Operculum absent. Tail heterocercal. Skeleton cartilaginous. Heart with a contractile conus arteriosus. Spiral valve in the intestine. Optic nerves not decussating or only partly decussating.
  A. Plagiostomi (sharks and rays).
  B. Holocephali (*Chimæra*).

II. Teleostomi.—Mouth terminal. Body usually covered with cycloid or ctenoid scales. Operculum present. Tail usually homocercal. Spiral valve usually absent. Skeleton contains bone corpuscles. Optic nerves decussating.
  A. Actinopterygii.
    1. Chondrostei (sturgeon).
    2. Holostei (garpike).
    3. Teleosti (bony fishes generally).
  B. Crossopterygii (*Polypterus*).

III. Dipnoi.—Have two pairs of nostrils. Breathe by gills or swim-bladder (*Ceratodus*, *Protopterus*, *Lepidosiren*).

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* For further details as to classification, characters, &c., the reader is referred to the Cambridge Natural History, "Fishes," or to any standard text-book of zoology.

The Cyclostomata comprise the lampreys and the very peculiar parasitic fish, the *Myxine* and *Bdellostoma*, which bore their way into the bodies of other fish, the cod being often attacked by the *Myxine*. The lampreys are also predatory, attaching themselves by their sucking mouth to the bodies of other fish, from which they scrape off the flesh. As the name implies, they have a circular mouth, the margins of which are beset with rows of small conical teeth, there being two larger blade-shaped teeth in the centre, sometimes called from their relative position the mandibular and maxillary teeth.

Until comparatively recently little was known of the structure of horny teeth, but they have been investigated by Beard ([1], [2]), who finds that the horny cone rests upon a slight dermal papilla, and fits into special epidermal depressions at the base of the papilla (in *Petromyzon fluviatilis*); but in *P. marinus* there are superimposed cones "like a nest of Chinese boxes." Each of these layers arises from a separate epidermal depression, which goes on continually forming horn, so that the under-cones are in no sense reserve teeth, for as each tooth is worn away at the apex fresh horny matter is formed below and pushed superficially. There is thus no resemblance to the teeth of higher vertebrates.

In a young lamprey there are to be found what at first sight look like true tooth-sacs, but the dental papilla never forms any odontoblasts, and the epithelium which corresponds to the enamel-organ produces horn. This is true of the marginal teeth, but further in towards the centre the teeth are formed simply in the basal layers of the epithelium, without the intervention of any sort of tooth-sac.

But in the *Myxine* and *Bdellostoma* there is an interesting arrangement of structures. They have a large sharply pointed median tooth and two comb-like smaller teeth upon the tongue, and the working surface of the teeth is composed of horn similar both in structure and development to that found in the lamprey.

Beard ([1], [2]) had described the tooth of *Bdellostoma* as consisting of a cap of horn, thick and strong, and of a bright yellow colour. Beneath this comes a layer of epithelium, and next to this a hard calcified material, which he regarded as some form of dentine. Some doubt, however, has been thrown upon the nature of this calcified dentine by the late Prof. Howes ([5]), and by Warren ([10]).

The horny cap is fitted into an epithelial groove at its base, so that it increases in length by the cells of this groove becoming cornified, and in thickness by a similar conversion of the epithelial layer beneath it.

The hard cone which forms, so to speak, the body of the subjacent tooth, Beard supposed it to be an anomalous structure, not closely corresponding with any known form of dentine, but yet being the product of an odontoblast layer upon the pulp, which latter remains in the base of the cone of dentine in the usual way.

The great hardness of the tooth and of the horny cap renders it a very difficult matter to obtain good sections, and hence the minute structure is difficult to determine. There is a layer of epithelium, in the proper situation, having the characters of an enamel-organ in so far as the presence of long columnar cells is concerned. But Warren, who investigated it later, strongly affirms that there is no real calcification, but merely a succession of horny caps superimposed on one another and developed from an epithelial groove after the usual manner of horny teeth. Were Beard's view correct, it would be difficult to conceive that the presence of the calcified cap could be of much, if any, service whilst buried beneath the horny cap, and we should regard these structures not as an early and simple form of tooth, but as being degenerated teeth. They would thus lend support to the idea, already held by some, that these fish had as ancestors fish which had jaws, and teeth carried upon them. Marett Tims (7) has suggested the possibility of the derivation of the horny teeth of the Cyclostomes from the scales of the Teleostomi.

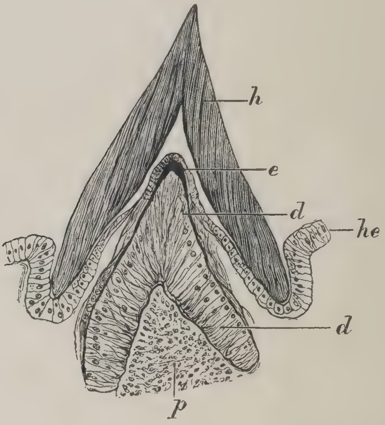

Fig. 159.—Tooth of *Bdellostoma*, semi-diagrammatic, after Dr. Beard. *d*. Calcified dentine cap. *e*. (?) Enamel. *h*. Horny tooth. *he*. Epithelial groove in which the base is formed.

It is to be noted that the relation, described by Beard, which the horny cone bears to the dental papilla and its dentine, is entirely different from that borne by the horny teeth of *Ornithorhynchus*, in which animal the horny plate, which replaces the teeth in the adult, lies beneath the teeth.

It has been suggested by Beard that the fusion of the lingual teeth of *Myxine* into a serrated horny plate may indicate the manner in which the serrated horny jaws of chelonians may have originated, as a substitution of horny tissue for true teeth upon which they were once superimposed. Similar speculations have been indulged in as to the manner in which the bird's bill may have originated from the substitution of a number of coalescent horny teeth for true teeth, but the material for such generalisation is not yet to hand. But, as has already been mentioned, no little doubt rests on this determination of structures, and it is now thought that these teeth are entirely horny.

Elasmobranchii.—As in the matter of teeth the *Palæichthyes*, or *Elasmobranchii*, comprising the sharks and rays and the ganoid fish, present somewhat simpler conditions than are met with in the osseous fish, it will be convenient to describe their teeth first.

In sharks the scales of other fish are represented by calcified papillæ, which have much the same structure as their teeth; to these the "shagreen," as shark skin is termed, owes its roughness. The mouth is a transverse, more or less curved fissure, opening upon the under-surface of the head at some little distance behind the end of the snout. Hence it is that a shark in seizing its prey turns over upon its back, or at all events upon its side.

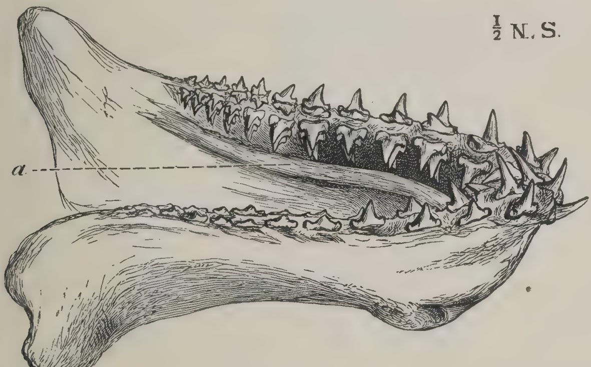

Fig. 160.—Lower jaw of *Lamna*. *a*. Edge of flap of mucous membrane which covers the teeth not yet completed.

The jaws, which are made up of the representatives of the palatoquadrate arch and of Meckel's cartilage, neither true maxillæ nor premaxillæ being present, are cartilaginous in the main, and therefore shrink and become much distorted in drying. The shape of the jaws differs in the various groups of *Plagiostomi:* in some each of the two jaws forms a tolerably perfect semicircle, while in others they are nearly straight and parallel to one another (see Fig. 160 and Fig. 164); but in all the rounded working surface of the jaw is clothed or encased by teeth, arranged in many parallel concentric rows.

The teeth which are situated upon the edge or exposed border of the jaw are usually erect, whilst the rows which lie behind them, farther within the mouth, point backwards, and are more or less recumbent, not having yet come into full use.

In this respect, however, marked difference exists among various genera of sharks; for instance, in the great tropical white shark the teeth which lie on the border of the jaw are erect, and all the successive rows are quite recumbent; whereas in many of the dog-fish the inner aspect of the jaws forms an even rounded surface along which the rows of teeth are disposed in every intermediate position between those fully recumbent at the innermost part of the jaw and those fully erected upon its exposed borders. Only a few of the most forward rows of teeth are exposed, a fold or flap of mucous membrane covering in teeth which are not as yet fully calcified and firmly attached to the gums.

In *Lamna*, which may be taken as fairly illustrative, the teeth are arranged round the jaws in concentric rows with great regularity, those of the successive rows corresponding in position to the teeth of older rows, and not, as is the case in some other sharks, to their interspaces. They are attached by being imbedded in a densely fibrous gum, which closely embraces their bifurcated bases; and this dense gum, carrying the teeth with it, slides bodily upwards over the inner face of the jaw, and outwards over its border, beyond which, to borrow a phrase from geological science, it has an "out-crop." The second and third rows of teeth are only partially erect, the rows behind these lying recumbent, and being in the fresh state covered in by the fold of mucous membrane, which, being dried and shrunk in the specimen figured, falls far short of its original level.

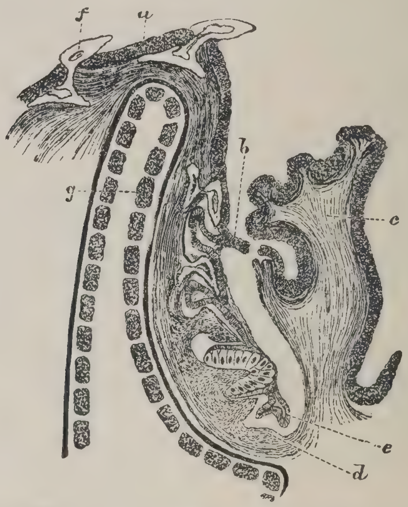

Fig. 161.—Transverse section of lower jaw of a dog-fish. *a.* Oral epithelium. *b.* Oral epithelium passing on to flap, from which it is torn in the figure. *c.* Protecting flap of mucous membrane (thecal fold). *d.* Youngest dentine pulp. *e.* Youngest enamel-organ. *f.* Tooth about to be shed. *g.* Calcified crust of jaw.

Thus rows of teeth, originally developed at the base of the jaw, are carried upwards, come to occupy the foremost position on the border of the jaw and are cast off when they pass the point *f* in the figure. It is thus easy to understand why shark's teeth are so abundantly found in a fossil condition, although other indications of the existence of the fish are comparatively rare; for every shark in the course of its life casts off great numbers of teeth, which fall to the bottom of the sea and become imbedded in the deposit there forming.

The teeth are never anchylosed to the jaw, nor have they any direct connection with it, but, as before mentioned, are retained by being imbedded in a very tough fibrous membrane. The nature of their fixation has been more exactly described on another page (p. 232).

It may be worth while to condense from Professor Owen the description of the manner in which it was proved that an actual sliding or rotation of the membrane does really take place, and that the whole jaw itself does not become slowly everted. The spine of a sting ray had been driven through the lower jaw of a shark (*Galeus*), passing between two (vertical) rows of teeth which had not yet been brought into use; when the specimen came under observation the spine had remained in this situation, transfixing the jaw, for a long time, as was evidenced by all the teeth of these two rows, both above and below it, being stunted and smaller than their neighbours. Hence the development of these teeth, which ultimately came to be at some little distance from the spine, had been profoundly modified by its presence, and it is difficult to understand in what manner this could have affected them had they not, at an earlier period of their growth, lain in more immediate proximity to it. But if the membrane with the teeth attached did move slowly along the surface of the jaw, this difficulty at once disappears.

The forms of the teeth in various sharks, though different and characteristic, nevertheless vary somewhat with age in some species, and present differences in size and form in the upper and lower jaws, or in different parts of the mouth of the same individual. For instance, in *Lamna* in the upper jaw the teeth of the third vertical row, counting from the middle line, are very small, while in both jaws there is a gradual diminution in the size of the teeth towards the back of the mouth. Moreover, many of the skates and rays exhibit sexual differences in their dentitions, in the male the teeth being simple and pointed, whereas in the female they may present a plate-like character. Thus, although it is often possible to refer a particular tooth to its right genus or even species, much care is requisite in so doing.

The teeth of the bloodthirsty white shark (*Carcharias*) are triangular flattened plates, rounded on their posterior aspect, with trenchant, slightly serrated edges. It has been pointed out by Owen that if the relation between the size of the teeth and that of the body were the same in extinct as in recent sharks, the dimensions of the teeth of the tertiary *Carcharodon* would indicate the existence of sharks as large as whales.

The intimate relationship between the teeth and the dermal spines, which, from the standpoint of development, has been illustrated at p. 3 and pp. 135 and 149, is apparent also in their histological structure. There are many dermal spines to be met with in the sharks and on the back or tail of rays, which seen alone could not possibly be distinguished from teeth, the resemblance both in outer form, in minute structure, and manner of development being most complete. The tooth figured on p. 105 is a fair example of a structure very common among the sharks, viz., a central body of osteodentine, the outer portion of which is covered by an enamel (?) of peculiar structure. Fine-tubed dentine is, however, also frequently met with, as is the case of the genus *Carcharias*.

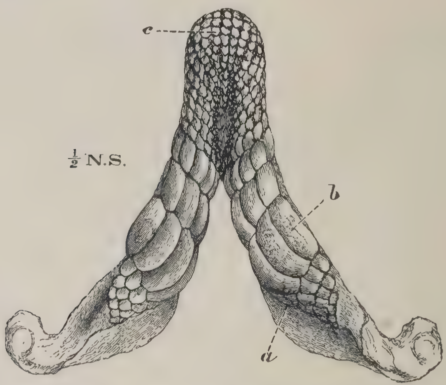

Fig. 162.—Lower jaw of *Cestracion philippi* (*Heterodontus*). *a*. Young teeth not yet in use. *b*. Large grinding back teeth. *c*. Small pointed front teeth.

The new teeth are developed at the bottom of the series on the inner side, and, just as in other sharks, are covered in by a flap of mucous membrane.

Dental tissues occur in other parts of the mouths of Plagiostomes than upon the jaws, not only in the embryonic stages, but in the adult. Thus Professor Sir W. Turner has described (^{9}) very numerous comb-like appendages five inches in length upon the branchial arches of the Basking-shark (*Selache maxima*) which apparently perform the same function as whalebone in straining the water. These combs are formed of a variety of dentine (? osteodentine), and closely resemble in structure the true teeth, which are, however, very small in this shark.

In the seas of Australia there exists a shark, the *Cestracion philippi*, with a very aberrant dentition, to which great interest attaches, inasmuch as it is the sole surviving representative of forms once spread all over the world. In the front of the mouth the teeth are small and very numerous; they are flat plates fitted by their edges to one another, while from their centres spring up sharp points, soon worn off when the tooth reaches such a position upon the jaw that it comes into use.

Proceeding backwards, the teeth cease to be pointed, increase in size, and become fewer in each row; a reference to the figure will convey a better idea of their general form than any description. Those which have come into use are, towards the back of the mouth, always much worn; their shedding and renewal takes place, as in other sharks, by a rotation of the mucous membrane over the surface of the jaw, so that, as might have been expected, large numbers of the isolated fossil teeth of Cestracionts are to be met with.

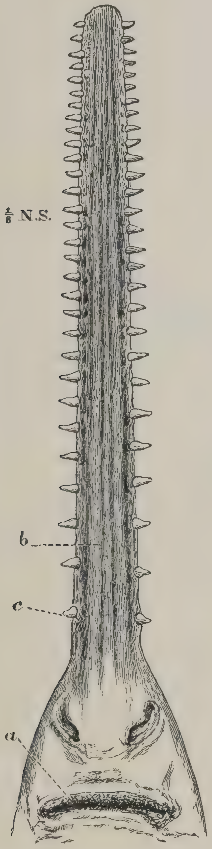

Fig. 163.—Rostrum and under-side of the head of a small *Pristis*. *a*. Mouth. *b*. Rostrum. *c*. One of the rostral teeth.

The teeth, with which the margins of the jaw are covered, are so small that they cannot be represented in this figure.

The teeth of *Cestracion* are fitted for the trituration of hard substances, and for such they are used, its food consisting of shell-fish, &c. They consist of a body of dentine partaking of the character of osteo- rather than of vaso-dentine, whilst the surface-layer is made up of sharply defined layers of fine parallel tubes, curiously gathered into bundles, which taper both towards the surface and towards the deeper part of the tooth. A comparison with other selachian teeth indicates that this layer may be regarded as a curiously modified enamel (p. 65).

The extinct Cestracionts extended far back in time, being met with in palæozoic strata. They were equally widely distributed in space. The size of many of the teeth indicates the existence of forms much larger than the recent timid and inoffensive *Cestracion philippi*. Many of the extinct forms are known only by isolated teeth; of others portions of the jaw with teeth *in situ* have been discovered; thus fragments of the jaw of *Acrodus*, the isolated fossil teeth of which have been compared to fossil leeches, with seven teeth arranged in series, have been met with.

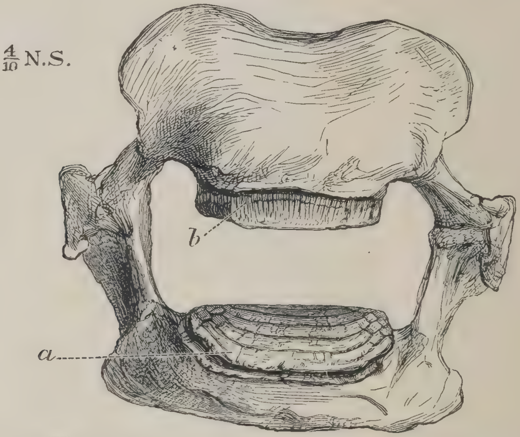

FIG. 164.—Upper and lower jaws of *Myliobates*. At *a*, the mosaic pavement formed by the broad flattened plates which constitute its teeth is seen, these being the oldest teeth which are about to be shed off in consequence of the rotation of the whole sheet of mucous membrane over the surface of the jaws. The letter *b* indicates the under-surface of one of the plates, which is seen to be finely fluted on its edges.

The *Pristis*, or saw-fish, so far as the mouth is concerned, is in no way remarkable, its teeth being small and blunt, like those of many rays. The snout is, however, prolonged to an enormous length, and is shaped like a gigantic spatula, its thin edges being beset by dermal spines of large size, arranged at regular intervals, and implanted in distinct sockets. These dermal spines, or rostral teeth, as they are sometimes termed, are not shed and replaced, but grow from persistent pulps. In structure they somewhat closely resemble the teeth of *Myliobates* (see p. 95), being made up of parallel denticles, in the centre of each of which is a pulp cavity or medullary canal.

What use the saw-fish makes of its armed snout is not very certainly known, but its rostral teeth are of interest to the odontologist for several reasons, one being that they are dermal spines, having a structure all but identical with that of the actual teeth of another ray, the *Myliobates,* while the scales of *Pristis* have a structure such that it is easy to imagine that these large spines are an aggregation of a number of the ordinary scales, enlarged and fused together. A second point of interest is that they are socketed, a manner of implantation not at all common amongst the teeth of fishes; and yet another is that they grow from persistent pulps, also unusual in fishes.

Broadly speaking, the teeth of the rays (skates) differ from those of typical sharks by being individually blunter, and being more closely set, so that they form something approaching to a continuous pavement over the jaws, with but little interspace left between the teeth.

The dentigerous surface of the jaw is very much rounded, and in some is completely encased under a pavement of teeth. Thus in *Myliobates* the powerful jaws are straight from side to side, while their working surfaces from back to front are segments of a circle. The teeth form a thick and strong pavement over the jaws, the manner of their formation and renewal conforming with the teeth of other *Plagiostomi.* The severe use to which they are put is indicated by the extent to which the grinding surfaces of those teeth which have come into use are worn down.

Several genera have the jaws thus covered, the number of the teeth differing; thus *Myliobates* has a central series of very broad, oblong teeth, to the outer sides of which are three rows of small hexagonal teeth. In *Œtobatis* the large oblong central plates constitute the whole armature of the jaw.

Amongst ganoid fish (*Chondrostei*) great diversity of dentition exists. Thus the sturgeons have no teeth, the mouth being at the lower surface of the snout, and being protrusible as a sort of suctorial tube. In the larval stages, however, the sturgeon possessed teeth. In the allied *Spatularia* there are numerous minute teeth, whilst there are many extinct ganoids with large blunt-pointed teeth upon the palate and mandible.

The American *Lepidosteus*, the structure of whose teeth has been described on p. 92, has a long pointed snout furnished with large sharp conical teeth.

Some of the extinct ganoids, *e.g.*, *Dendrodus* and *Rhizodus*, had conical teeth of reptilian appearance. Others combined chisel-shaped teeth in front with large hemispherical or flattened teeth on the palate and part of lower jaw, whilst others again were only furnished with crushing teeth.

The great majority of ganoid fish are extinct, and it is now claimed that these extinct forms link the ganoids directly with the Teleostei, or osseous fishes.

The **Dipnoi,** or lung fishes, which are able to breathe for periods out of the water, present some resemblance to the Amphibia. *Lepidosiren* has a peculiar dental armature, the margins of the jaws being formed by serrated plates anchylosed to the bone. These plates have upon their edges five deep angular notches, the prominence of the upper plate corresponding to the notches of the lower; and the edge is kept somewhat sharp by the disposition of the hard tissues.

On the edge of the bone lie superimposed layers of a tissue which appears to be enamel, and a blunt edge is kept up by these resisting wear longer than the bone in which they are imbedded. The attention of the author was called to this structure by Mr. Leon Williams, and of which there appears to be no published description.

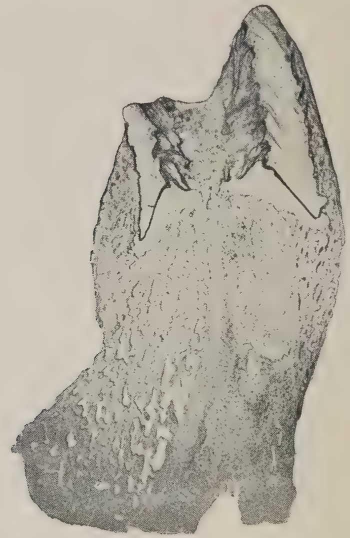

FIG. 165.—Edge of jaw of *Lepidosiren*, in which are developed superimposed plates of enamel. Prepared and photographed by Mr. Leon Williams.

The cutting plates of the upper jaw are developed near the median line of the palate and on the palate bones, and in front of them there are conical piercing teeth upon that forward prolongation of the cartilage which takes the place of a distinct vomer; these have sometimes been described as being upon the nasal bone. It would seem that the two conical piercing teeth serve as holdfasts, while the cutting edges of the deeply notched plates are brought into play to slice up the food.

Both in structure and general disposition the dental plates in *Lepidosiren* are paralleled by the teeth of *Ceratodus*, for some time known only as a fossil, but of which recent examples have been captured in Queensland; this resemblance was suspected some years ago by the late Professor Moseley, before the affinities of *Ceratodus* were known.

Semon (6) has shown that the vomerine and palatine teeth originate as distinct rounded tubercles, corresponding to the roots of the adult tooth. The dental plates are thus shown to be the result of concrescence, of the fusion of teeth at first separate.

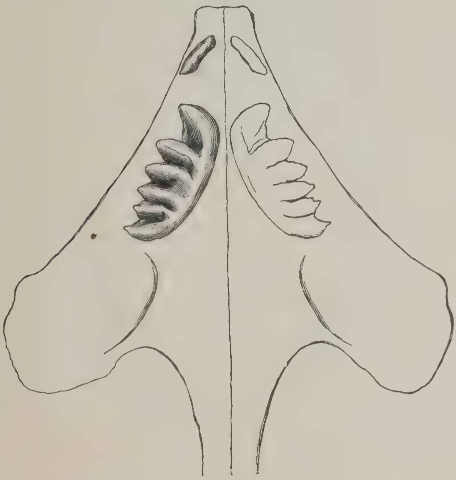

FIG. 166.—Upper jaw of *Ceratodus*. From a recent specimen.

A somewhat similar condition exists in *Phyllodus*, an extinct fish from the London clay, known only by its teeth, and referred to the Wrasse family. In this there are superimposed layers of dentine and enamel not imbedded in bone. The dentine is, however, in very small proportion, and a still further reduction in the dentine would bring it very much to the condition of the enamel plates of *Lepidosiren*, so that this explains the apparent anomaly of successive plates of enamel developed without dentine. This structure is unlike that found in recent Wrasses, and suggests doubt as to the affinities of *Phyllodus*.

The **Teleostei**, or osseous fish, form the group which comprises all the fish most familiarly known to us, and within its limits the variation in dentitions is so great that few, if any, general statements can be made about them. It is not uncommon to find teeth crowded upon every one of the bones which form a part of the bony framework of the mouth and pharynx, and the teeth are sometimes in countless numbers. [Tooth-like structures are even found in the œsophagus of *Centrolophus ovalis* and other members of the family *Stromatidæ*. Thornton Carter has also demonstrated recently the presence of true denticles on the snout of *Xiphias gladius* (4).] Such is the variability that even within the limits of single families great differences in the teeth are to be found.

The teeth of fish are of all degrees of size and of fineness. In some (Chætodonts) the teeth are as fine as hairs, and are so soft as to be flexible; they formerly were supposed to be horny, but the larger ones are composed of a vascular dentine surmounted at the tip by a curious little hook of enamel.

In the finest teeth there is hardly room for vascular canals, but no one can doubt their derivation from the larger forms, so that the idea that these teeth are horny must be abandoned *in toto*.

Teeth which are very fine and very closely set are termed "dents en velours," "ciliiform" or "setiform"; when they are a little stouter, "dents en brosse," or "villiform," and when still stronger and sharper, "dents en cardes." Teeth that are conical, wedge-shaped, spheroidal, and lamelliform, are all to be met with.

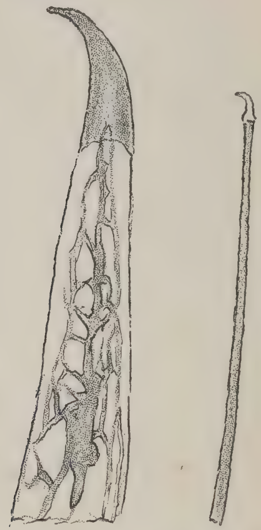

Fig. 167.—Teeth of a species of *Chætodon*. The recurved enamel tips are apparently structureless.

And there are some fish, *e.g.*, some of the large Siluroids, which have very strong, large teeth, an inch and a half or more long, and very firmly anchylosed to the bone.

The long and very strong snout of the sword-fish, formed by a coalescence of the maxillary and intermaxillary bones, which is able to pierce a plank, is roughened on its lower surface by villiform teeth which can be of no use, and are therefore to be regarded as rudimentary survivals.

In the common pike the mouth is crowded with sharply pointed teeth, having a general inclination backwards, and being in some parts of the mouth of larger size than in others. The margin of the lower jaw is armed with teeth of formidable size and sharpness, the smallest teeth being at the front, where they are arranged in several rows, and the largest being about the middle of the side of the jaw. A pike, as is well known to anglers, when it has seized a fish, often holds it across its mouth, piercing and retaining it by means of these largest teeth; then, after holding it thus for a time, and so having maimed it and lessened its power of escape, it swallows it, generally head foremost. The tenacity of the pike's hold is often illustrated when it takes a bait, and retains it so firmly that when the angler "strikes" the hooks do not get driven into the fish's mouth; but after tugging at the bait for a time the pike releases it, and the angler finds that it has never been hooked at all.

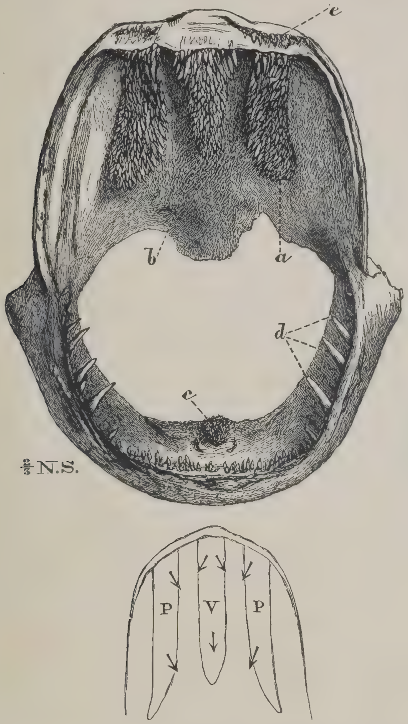

Fig. 168.—Jaws of a pike, viewed from the front, with the mouth opened more widely than is natural, so as to bring the teeth into view. *a*. Group of teeth situated on the palatine bone. *b*. Group of teeth situated on the vomer. *c*. Group of teeth situated on the lingual bone. *d*. Specially large teeth, placed at intervals round the margin of the lower jaw. *e*. Group of teeth on the intermaxillary bones.

The diagram represents the direction in which the hinged teeth of the vomerine and palatine bands can bend.

The margin of the upper jaw is not bordered by teeth, save at the front, where the intermaxillary bones carry a few teeth of insignificant dimensions; indeed, it is rather exceptional for the true maxillary bones to carry teeth in osseous fish. The roof of the mouth presents three wide parallel bands of teeth, those in the median band (on the vomer) being directed backwards, those upon the lateral bands (on the palatine bones) backwards and inwards. Some of the latter teeth are very large, but not quite so large as those at the sides of the lower jaw.

The marginal teeth are firmly anchylosed, but the teeth upon the palate are all hinged, and in such a manner that they can only bend exactly in one direction. Those of the vomerine band which lie in the middle line will bend backwards only; those upon the outer margins of this band backwards, with an inclination outwards. Those of the lateral or palatine bands bend obliquely backwards and inwards, at an angle of about 45° with the median line of the mouth, or somewhat more directly backwards. To a body sliding over them in one direction they offer no resistance, bending down as it passes, and springing up as the pressure is removed from them, but to anything moving in any other direction they are rigidly fixed sharp curved stakes, impeding its further progress.

An elongated body of some size, such as a living fish, can only be swallowed by the pike when it is arranged lengthwise in the mouth; crosswise it cannot possibly enter the throat. The hinged teeth on the palate seem admirably arranged for getting the fish into a longitudinal position and keeping it there; for if we imagine the fish's body held up against these teeth, and consider the direction in which the hinging of the teeth allows them to yield, it will be seen that every motion tending to arrange the body lengthwise, either in the median line of the mouth or in either of the interspaces between the vomerine and palatine bands of teeth, will meet with no obstruction, but in every deviation from this position it will be caught on the points of the teeth and resisted. Thus with the pike's mouth shut, and the prey kept up against the palatine teeth, even its own struggles will be utilised by allowing every movement tending to place it aright, and every other being stopped by the bands of hinged teeth entangling it. The structure of these teeth, and the mechanism by which they are rendered elastic, have been already described (p. 235).

The lingual bone, and the three median bones behind it, carry small teeth arranged in oblong patches; the internal surfaces of the branchial bones (which support the gills) are armed with similar small teeth; while the last or fifth branchial arch (which carries no gills, the bones forming it being called inferior pharyngeal bones) possesses larger teeth. The superior pharyngeal bones (which are median portions of the four anterior branchial arches) also carry recurved teeth larger than those which line the rest of the internal surfaces of each of the branchial arches.

The pike's mouth and pharynx thus fairly bristle with teeth, all directed somewhat backwards; and any one who has been unfortunate enough to have allowed his fingers to get entangled in the mouth of a living pike will realise how small a chance of escape its living prey has when once it has been seized.

The teeth of the pike are composed of a central body of osteodentine, on the outside of which is a layer in which the dentinal tubes are directed towards the surface, as in hard or unvascular dentine (see Fig. 76); while the outermost portion of all is a very dense and hard film, which is perhaps enamel. The teeth are anchylosed to the bone, and are very frequently renewed, their successors being developed at one side of their bases (cf. p. 275).

Though the pike has rather more teeth than many other fish, it may be taken as a fair example of most osseous fishes in this respect. Space will only allow of a few of the more exceptional forms being here described.

The angler (*Lophius piscatorius*), another predatory fish, found on our own coasts, with an enormous mouth and disproportionately small body and tail, lies hidden in the mud, or crouched upon the bottom, and makes a rush upon smaller fishes which approach sufficiently near to it. It is remarkable for the manner of attachment of the teeth, some of the largest of which upon the edges of its jaws do not become anchylosed, but are so attached, as has been described at p. 233, as to allow of their bending inwards towards the mouth, but not in the opposite or indeed any other direction. The teeth of the outer row are firmly anchylosed to the margins of the jaw, and the far larger hinged teeth form a sort of irregular second row.

The benefit of such an arrangement to a fish of its habit is sufficiently obvious: its teeth allow the utmost freedom of entry, but offer obstacles to anything getting out again.

This arrangement of teeth, long supposed to be unique, is closely paralleled in a very different fish, the hake (*Merlucius*, one of the *Gadidæ*). This fish, the most active and predatory of the cod family, follows shoals of pilchards and of herrings, themselves active fish, and feeds upon them. The margins of the jaws carry two distinct and regularly arranged rows of teeth, an outer smaller row which are anchylosed, and an inner longer row which are hinged. They are very sharp, being tipped with spear points of enamel, and are recurved. In the fresh state they look quite red, being composed of a richly vascular vaso-dentine.

The family of *Gadidæ* or cod fishes, which the best authorities state to be a well-defined and natural group, present an interesting series of gradations between teeth immovably fixed, teeth admitting of slight motion, and highly specialised hinged teeth such as those of the hake. The author has examined the teeth of a considerable number of *Gadidæ* (7) and found that they presented wide variability in the structure of their teeth; at the same time these differences are linked together by every gradation. Thus are seen the rich and regular disposition of vascular canals in the ling and hake, the less abundant system of canals in the cod, whilst in the rock-cod (*Motella*) the dentine is laminated and contains few canals, and in *Lotella*, a fish found in Japan, and allied to the hake, there are no vascular canals and no dentinal tubes, but a strongly marked lamination is seen.

Whilst in members of the family which are very closely related there is a similarity of histological structure, the extent to which the vascular canals are present and the pattern in which they are arranged does not always accord in its variations with the generally accepted classification of the genera. Reduction in size does not imply simplification of structure, for the tiny teeth termed gill-rakers, which cover the inner surfaces of the gill arches of the hake, are identical in structure with its larger teeth, and, on the other hand, the very large teeth of *Uraleptus* are found to be quite simple in structure. It is difficult to understand by what process of selection differences of minute structure have been brought about, for it would seem as if from the point of view of efficiency it would matter little what the minute structure be so long as a tooth be strong enough and sharp enough. More detail on this subject will be found in the paper referred to (⁸).

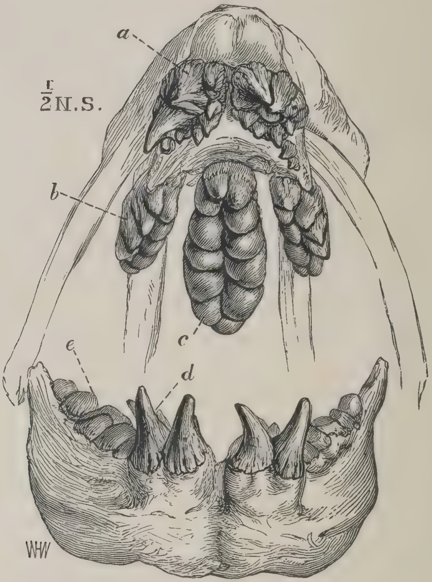

Fig. 169.—Bones of the mouth of the wolf-fish (*Anarrhichas lupus*). The letter *a* indicates the divergent pointed teeth which occupy the intermaxillary bone; the letter *d* indicates the similar teeth which are attached to the front of the mandible, on the middle and back parts of which are round-topped crushing teeth (*e*). Strong crushing teeth are found also upon the palatine bones (*b*), and upon the vomer (*c*).

In several of the deep sea fish dredged by the *Challenger* from depths to which light does not penetrate, hinged teeth have been found (cf. p. 234). Many of these deep sea fish have very formidable dental armaments, and, curiously enough, one of these, which has exceptionally long upper teeth, has a downward projection from the lower jaw, which serves to protect them while closed, an arrangement elsewhere only met with in extinct mammalia, such as *Dinoceras* and *Machairodus*, figured later on in this work.

All of them are carnivorous, the toothless forms feeding on animalculæ which live at great depths or sink down from lesser depths, and all are akin to forms which inhabit lesser depths from which the very deep sea fauna has been gradually modified. The dentition of many might be called eccentric, the teeth in front of the mouth being so long that in closure of the mouth they pass outside the opposite lip for a considerable distance. Sometimes these very long teeth are hinged; sometimes they are anchylosed.

Another curious dentition is possessed by the wolf-fish (*Anarrhichas lupus*), also an inhabitant of British waters, and sometimes to be seen in London fishmongers' shops under the name of the sea-cat. The intermaxillary teeth are conical, bluntly pointed, and set forwards and outwards; these are antagonised by somewhat similar teeth in the front of the lower jaw. The palatine bones carry short, bluntly conical, or round-topped crushing teeth in a double row; the vomer is also armed with a double row of very much larger and shorter teeth. The lower jaw, with the exception of its anterior part, is occupied by teeth of similar character.

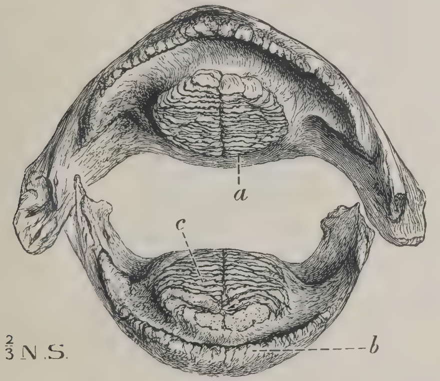

FIG. 170.—Jaws of the *Diodon*. *a*. Base of the dental plates, where new lamellæ of dentine are being developed. *b*. Margin of jaw, formed mainly by the sides of the denticles. *c*. Compound tooth, made up of the superimposed lamellæ of dentine anchylosed together.

All the teeth of the wolf-fish are anchylosed slightly to the bone, a definite process from which forms a sort of short pedestal for each tooth. The jaws are worked by muscles of great power, and it seldom happens that a specimen is examined in which some of the teeth are not broken. It feeds upon shell-fish, the hard coverings of which are crushed by the blunter teeth, while the pointed front teeth apparently serve to tear the shell-fish from the rocks to which they are commonly attached.

In the group of fish known as "Gymnodonts" (naked-toothed), the teeth and the margins of the dentigerous bones form a sort of beak, which is not covered by the lips. The example here figured consists of the upper and lower jaws of the *Diodon*, so called because it appears to casual observers to have but two teeth. A kindred fish, in which the division of each jaw in the middle line is conspicuous, is similarly called *Tetrodon*. The jaw consists of teeth and bone very intimately fused together; the broad rounded mass (*c* in the figure), which lies just inside the margin of the jaw, is made up of a number of horizontal plates of dentine, the edges of which crop out upon its posterior surface; and these are united to one another by the calcification of the last remains of the pulp of each plate into a sort of osteo-dentine, the different hardness of the two tissues keeping the surface constantly rough, as the plates become worn away. The whole margin of the jaw is similarly built up of smaller horizontally disposed denticles, or plates of dentine, which are, as they wear down, replaced by the development of fresh plates, which are added from beneath, where they are developed in cavities situated low down in the substance of the bone.

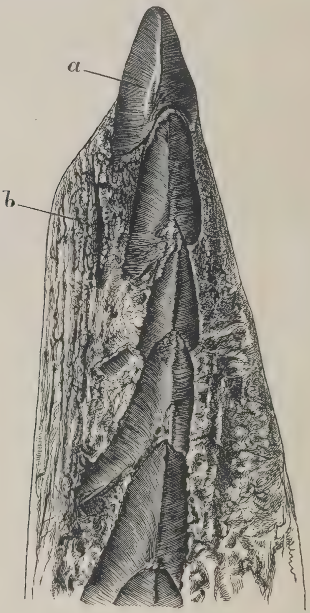

FIG. 171.—Edge of jaw of *Pseudoscarus* (?). *a*. Denticles. *b*. Bone of jaw.

The new teeth or plates of dentine thus formed at the base of the hemispherical masses within the jaws (at the point *a*), or low down in the substance of the jaw, do not come into use by the ordinary process of displacing their predecessors and themselves being in turn replaced, but fresh plates only come into use by the actual wearing away of all that is above them, both dentine and bone, so that they come to form the topmost portion of the jaw. The margins of the jaw are, however, mainly built up of dental tissues, there being but little bone in their interspaces.

Tetrodon has not the rounded triturating disc of the *Diodon*, or has it but feebly represented; and the margins of the jaws are sharper.

In the parrot-fishes (*Scarus*), which are very nearly allied to the gymnodonts, somewhat similar beaks are found, the individual teeth being more conspicuous. The whole outer surface of the jaw near to its working edge is covered by a sort of tesselated pavement, formed by the several teeth which are pressed together into a mass; these are placed only on the outer surface and the immediate edge, so that the soft bone is part of the working surface, or would be but that, by its more speedy wear, it leaves the edge, formed by dentine and enamel, always prominent and more or less sharp.

The structure and succession of these teeth have been carefully described by J. von Boas (^{3}), and the differences between the several genera pointed out. He describes cementum as binding the denticles together and forming a part of the working edge, but that which he describes as cementum appears to be that tissue which the author has termed "bone of attachment." See p. 238.

In a section of a jaw in the possession of the author, which he believed to have belonged to a gymnodont fish but which bears a remarkably close resemblance to that figured by von Boas as being a jaw of *Pseudoscarus*, a very beautiful arrangement serves to preserve the sharpness of the edge of the jaw.

The denticles are conical, and form a series of hollow superimposed cones with the points directed upwards. They consist of dentine and enamel, and the point of the subjacent cone fits into the hollow of that above it so closely that in von Boas' specimen the dentine of the older tooth is in great part absorbed to make way for the point of its successor; the working denticle thus comes to be little more than a hollow cone of enamel. This is not the case in the specimen referred to, in which there is a quantity of dentine left in each denticle. This vertical series of superimposed sharp cones lies in the midst of the somewhat thin jawbone, fused together by bone of attachment (? cementum), and enclosed between the inner and outer plates of the jaw.

The bone, being considerably softer than the dentine, wears down much faster, so that the edge is always formed by a prominent sharp tooth, which, as the wearing down of the bone progresses, falls off, and the next one beneath it comes into play. The arrangement recalls the way in which a scythe or a chisel is assisted in keeping its edge by being made of a plate of steel welded between two plates of softer iron.

The pharyngeal bones are also remarkable; the two lower are united into one, and the stout bone so formed is armed with teeth;

it is antagonised by two upper pharyngeal bones similarly armed. It carries teeth which are anchylosed to it, and which are so disposed as to keep the surface constantly rough. When they are freshly formed the teeth have flattened thin edges, something like human incisors. They are coated with enamel, and thus, when calcification has proceeded so far as to obliterate their central pulp cavities, after the tooth is worn to a certain point (*c* in Fig. 172) it presents a ring of enamel, inside which is a ring of dentine, and inside this a core of secondary dentine, as seen in the figure. Owing to the different hardness of the three tissues, a constant roughness of surface is maintained. The upper pharyngeals are similarly armed; and as the teeth and the supporting bone wear away fresh teeth are developed at the front, so that the whole bone undergoes a sort of gliding motion backwards, the armature of the lower pharyngeal being renewed in a similar manner, save that new teeth and bone are developed at its posterior instead of its anterior extremity.

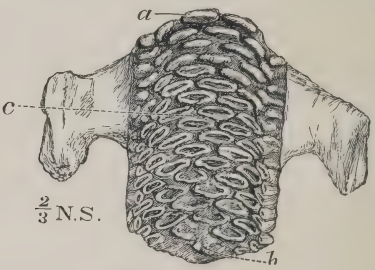

FIG. 172.—Lower pharyngeal bone of *Pseudoscarus*. *a*. Posterior border at which the teeth are unworn. *c*. Oval areas formed by teeth, the points of which are worn off. *b*. Anterior edge of bone, at which the teeth are almost completely worn away.

The teeth are developed in bony crypts, below the youngest functional teeth, and perforations in the roofs of the crypts give passage to the connecting band between the tooth-sac and the mucous membrane.

The sheep's-head fish (*Sargus*), to which attention has been drawn on account of the peculiarities of structure which it well exemplifies, has curiously human-like incisors in the front of the mouth, and round-topped crushing teeth inside.

No more fitting place will occur for noticing the stout pharyngeal teeth which are met with in so many fish.* Some fish, which are edentulous so far as the mouth proper is concerned, have the pharyngeal bones armed with teeth; in the carp and its allies, edentulous so far as the mouth proper is concerned, the two lower pharyngeal bones carry long pointed teeth, which partly oppose one another, and partly oppose a sort of horny tubercle, which is supported on a process of the base of the occipital bone.

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* For a more detailed account of the pharyngeal teeth of fishes the reader is referred to a series of papers by Colonel Shepherd in the *Zoologist* (H W. M. T.).

A few fish are quite without teeth; the sturgeon, whose mouth forms a protrusible sucker, is edentulous, as are also the pipe-fish and the little sea-horse (*Hippocampus*), now so common in aquaria. These are to be regarded as degenerations from ancestors which possessed teeth, and not as fish which have never from the earliest times acquired teeth.

As a rule fish are remarkable for the great number of their teeth, which are being constantly shed off and replaced by successors an indefinite number of times.

In all the fish hitherto mentioned in these pages, it happens that the teeth in different parts of the mouth differ in size and in the function which they have to perform, but this is only so because a few striking forms have been naturally selected for description. It is far commoner for all the teeth of fish, particularly of those fish which have countless numbers of teeth, to be very nearly alike in form and size in all parts of the mouth. Usually fish do not comminute their food very fully, but make use of their teeth simply for the prehension of prey, not submitting the food to any mastication whatever; their teeth are hence often mere sharp cones, slightly recurved, or set pointing backwards. Thus, though the mouth of the common pike is beset with an immense number of sharp teeth, its food is swallowed whole, and very often is alive when it reaches the stomach, the sole purpose served by the teeth being the prevention of its escape when once it has been seized.

Implantation of the teeth in sockets is not usual in the class of fish. Still many examples of it may be found; for example, the Barracuda pike (*Sphyræna*) has its lancet-shaped teeth implanted in distinct sockets, to the wall of which they are said to become slightly anchylosed; the file-fish and others might also be cited. And although the succession of teeth is usually from the side, in some cases the successional teeth are developed in alveolar cavities within the substance of the bone, and displace their predecessors in a vertical direction, as happens in the pharyngeal teeth of the wrasses, or the incisors of the sheep's-head fish (*Sargus*); *Lepidosteus* also has its teeth affixed in incomplete sockets, to the walls and bases of which they are anchylosed; this is not a very uncommon arrangement with the teeth of the fish when they are socketed at all.

As has been already mentioned, sexual differences may be met with between the teeth of the male and female, as in some species of skate, though such differences are by no means common. Although not, strictly speaking, a dental character, it may not be out of place to mention here the peculiar armature of the jaw of the male salmon at the breeding season.

The end of the lower jaw becomes prolonged, and turned upwards at its point; the stout cartilaginous hook thus formed is of such dimensions that it has to be accommodated during closure of the mouth in a deep cavity formed for it between the intermaxillary bones. In some Canadian salmon this process is supposed to be constant in the older males, but in the British fish it disappears, and only exists at the breeding season. After spawning it is still strongly developed, and the salmon is a foul fish and is called a kelt. It is used apparently as a battering-ram, and salmon are constantly found killed with their sides deeply gashed by the charges of their opponents.

Not much can be said in general terms of the structure of the teeth of fish. The bulk of the teeth of most fishes is made up of one or other modification of vaso-dentine or osteo-dentine; this is often glazed over upon its exterior by a thin film of enamel, so thin as often to appear structureless.

Unvascular dentine also forms the teeth of many fish, and in some is remarkable for the fineness of its tubes; in fact, every form of dentine, from fine-tubed hard dentine to tissue indistinguishable from coarse bone, is to be found in this class.

Dentine of very complex structure (labyrintho-dentine) is met with in some fish; and an example from the *Lepidosteus* (American garpike, a ganoid fish) has been figured on p. 92.

Enamel is often present in a very thin layer, glazing the exterior of the dentine; sometimes it forms a mere tip, a sort of spear-point to the tooth, as in the eel, the hake, and in chætodonts (see Figs. 153 and 167), and sometimes it is very thick, and itself permeated by systems of tubes (see Fig. 45).

Cementum is of comparatively rare occurrence in fish.

Professor Kölliker has shown that in a very large number of fishes the skeleton more nearly resembles dentine than true bone in its structure. This is especially the case upon its surface, the jaw of the wrasse, for instance, presenting a fine-tubed layer with no lacunæ or other irregular spaces; whilst the dermal scales and the protective spines of fish are made up of a tissue closely resembling dentine (cf. Professor Williamson (11)). We may say, then, that just as in the external skin bony or dentinal plates are developed for the purpose of protecting it from destruction by attrition, so for a similar purpose teeth are developed in that portion of the mucous membrane which covers the jaws.

With regard to their development (cf. pp. 134, 145, 149), it may be added that in an embryo pike the first teeth are formed in a primitive fashion, there being an upstanding dentine-papilla with so little specialisation of the surrounding epithelium that it resembles in its manner of formation a dermal placoid spine (Fig. 91), and so far invalidates the statement that the enamel-organ is always the first thing to appear. Though in most cases this simple condition afterwards gives way to the formation of tooth-germs of an ordinary type, situated more deeply in the submucous tissues, it to some extent persists in the case of the very small and numerous teeth found in some parts of the mouth.

A change in the methods of development after the appearance of the earliest teeth has been observed in other fish. Thus, the earliest tooth-germs of *Myliobates* are rounded and all alike, but in the second generation enlargement of the middle teeth occurs, without, it is said, any evidence of coalescence of several smaller ones, and the earliest teeth of *Cestracion* are all alike, and none resembles the flattened molariform teeth afterwards formed (Friedmann and Röse, as quoted by Burckhardt).

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CHAPTER XI.

THE TEETH OF AMPHIBIA, REPTILES, AND BIRDS.

In these classes the teeth are never so numerous nor so widely distributed upon the bones of the mouth as in fish. A double row of teeth arranged in concentric lines in the upper jaw, between which a single row of teeth upon the lower jaw passes when the mouth is closed, is an arrangement common amongst Amphibia. The outer of the two rows of teeth in the upper jaw is situated upon the premaxillary and maxillary bones, and usually extends further back than the vomerine or inner row. Almost all batrachians and reptiles have an endless succession of teeth, *i.e.* they are said to be *polyphyodont*; but there are some lizards (*e.g.* the chamæleon and *Hatteria*, now generally known as *Sphenodon*) in which no replacement takes place. Only a few reptiles (*e.g. Hatteria*, *Ophisaurus*, a snake-like lizard akin to the blindworm, chamæleon) have a row of vomerine teeth.

Amphibia.—From the type of dentition just described are many deviations; thus the toads are edentulous, and the frog has no teeth in the lower jaw.

The teeth of the frog form a single row upon the margin of the upper jaw, their points projecting but little above the surface of the mucous membrane, and the vomerine teeth are few in number and cover only a small space.

The edentulous lower jaw passes altogether inside the row of upper teeth, and having rounded surfaces and no lip, fits very closely against the inner sides of the teeth. Thus it leaves very little room for the young developing tooth-sacs, which are accommodated with the space required for the attainment of their full size, by the absorption of the older solid bone and of the tooth which has preceded them, in the following manner. The teeth are attached to the bone by anchylosis, each tooth being perched upon a little pedestal of bone specially formed for it. The successional teeth, the germs of which originally lay at the inner sides of the old teeth, commonly undermine the sides and bases of the pedestals of the latter, and move bodily beneath them, so that the new tooth completes its development in what was once the pulp cavity of its predecessor.

The teeth of the frog consist of a body of hard dentine, coated with an exceedingly thin layer of enamel, the existence of which has been doubted by some writers; but a study of the tissues of the tooth-sac renders it probable that the transparent layer, which is undoubtedly present, is really enamel.

The teeth of the newt and its ally the salamander are remarkable for having tips of enamel, somewhat like those of the eel (see Fig. 153), save that they are bifurcated, the one point being larger and longer than the other.

The armature of the mouth of the tadpole is peculiar and interesting. Upon its cartilaginous jaws are tough, horny plates, something in general shape like a turtle's bill; but in addition to these the inner margins of the lips are set with tiny horny spines or hooks seated upon expanded bases. The apices of these spines have frequently three minute points arranged longitudinally, the median point being the most pronounced.

Each one of these spines is the product of the cornification of a single epithelial cell, which has become of very large size and shaped into an extinguisher-like form. Beneath the one in use are a number of others in serial stages, ready to succeed when the top one falls off. The beaks are formed in exactly the same way, save that, the cells being closely placed side by side, a continuous sheet is formed instead of isolated spines. These horny cases are shed off prior to the commencement of true tooth formation.

Some extinct Batrachia were of large size; the *Labyrinthodon*, the structure of whose teeth has already been described (p. 93), was furnished with a marginal row of teeth in the upper jaw, of which some few were of larger size and greater length than the others. In the lower jaw, the teeth, which are similar to those of the upper, are disposed in some sense in an incomplete double row, the series of smaller teeth not being interrupted by the occurrence of the larger tusks, but passing in unbroken series outside them. The *Labyrinthodon* was possessed also of palatine teeth.

The teeth were anchylosed to slight depressions or sockets, and the successional teeth were probably developed, as in the frog, at the inner side of the bases of the teeth already in position, as there are no indications of crypts within the bone.

Reptilia.—In many reptiles teeth are developed for the merely temporary end of effecting an exit from the egg-shell. This purpose is sufficiently answered by the hard snout of the crocodiles and by a sort of snout developed in Chelonia, but snakes and lizards have sharp teeth, developed on the premaxillary bones, which are afterwards lost, and these are true teeth, formed of dentine.

(i.) The **Chelonia,** comprising the tortoises and turtles, have no teeth, but the margins of the jaws are sheathed in horny cases, variously shaped in accordance with the habits of the animal, being sharp and thin-edged in carnivorous and blunt and rugged in herbivorous species.

It is stated by Röse that a tooth band exists, but that it does not go on to the formation of any definite tooth-germ rudiment.

Some extinct forms of reptiles, the flying dragons (*Ornithosauria*), were also devoid of teeth, and had very bird-like beaks, presumably covered with horn.

It is difficult to make any very general statements as to the teeth of reptiles, as so large a variety exists. Many, however, have simple conical teeth, either attached in grooves as in the great extinct fish-lizards (*Ichthyosaurus*), in distinct sockets as in the crocodiles, or anchylosed by their sides or by their bases to the bone, as in most lizards. Usually they are confined to the margins of the jaws, but, as already mentioned, a second row of vomerine teeth sometimes exists. Less commonly, palatal teeth, flattened to form a sort of pavement to the roof of the mouth, are met with; such are to be found in several extinct reptiles. In structure many of them consist of a fine-tubed dentine, with a coat of enamel, also of simple structure, but there are not wanting teeth of very complex structure, similar to those found in *Labyrinthodon* among Batrachia. The complexity of pattern arises, however, more from the existence of plici-dentines than of vascular dentines, although in some, for example the *Iguanodon*, there are medullary channels arranged with regularity.

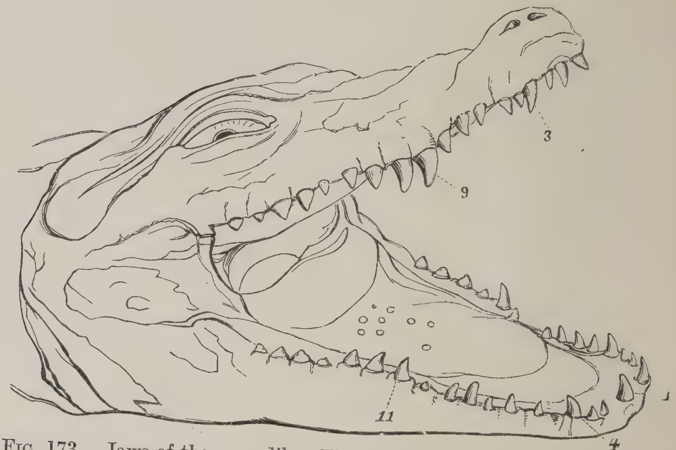

FIG. 173.—Jaws of the crocodile. The first, fourth, and eleventh teeth in the lower jaw, and the third and ninth in the upper, are seen to attain to a larger size than the others.

(ii.) In **Crocodilia** the teeth are confined to the margins of the jaws, where they are very formidable in size and sharpness. The individual teeth are generally conical, sharply pointed, *i.e.*, *haplodont*, and often a little compressed from side to side, so as to possess sharp edges; but they vary much in form in different species.

[Bolk has thrown doubt on the generally accepted view that the haplodont type of tooth found in the crocodiles is a primitive pattern (2, a, b). In his opinion this type of tooth is as much secondary as is the haplodont tooth of the Odontoceti. According to Bolk, the primitive reptilian type is a tricuspidate tooth, sharp-edged and compressed from side to side. Such a tooth he found in the embryo of

Crocodilus porosus ; these embryonic teeth do not cut the gum, are never functional, and are succeeded by a second set of styliform teeth. Such tricuspidate teeth are to be found in the majority of reptiles. These conclusions of Bolk's are confirmed by his pupil Woerdeman in a long and careful paper on the development of the teeth in a large number of reptiles (16). This subject is of considerable importance in view of Bolk's suggestions as to the evolution of the molar patterns in the mammalia, and to which reference will be made subsequently (Chapter XIII.).]

The teeth are lodged in distinct tubular alveolar cavities (thecodont), to the walls of which they do not become anchylosed. They are tolerably constant in number in the same species.

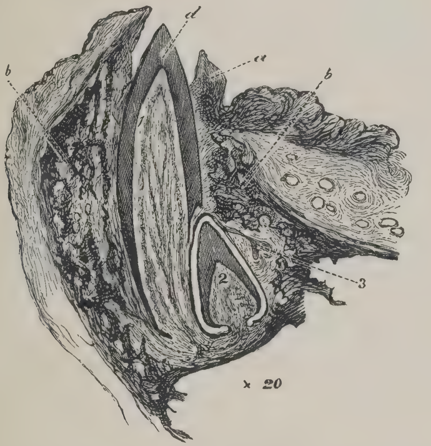

Fig. 174.—Transverse section of the lower jaw of a young alligator. *a.* Oral epithelium. *b.* Bone of socket. *d.* Dentine of old tooth. 2. Tooth next in order of succession, which is causing absorption of one side of the base of the older tooth. 3. Young tooth-germ.

In parts of the mouth certain teeth are developed to a greater length than those nearest to them ; thus, in the crocodile proper, the first and fourth lower and the third and ninth upper teeth are specially large. This character is common to alligators and many true crocodiles, the former being distinguished by the first and fourth lower teeth being received into deep pits in the upper jaw.*

The garial, or slender-snouted crocodile of the Ganges, has long and very narrow jaws, with slender recurved teeth, its jaws recalling those of a dolphin, like which it feeds exclusively on fish and, although the creature may attain to the length of 20 feet, is not dangerous to mammals. Various crocodiles are intermediate in respect of the length and width of their jaws between the garial and the broad-nosed alligator.

* It is doubtful whether these distinctions are characteristic.—Ed.

In structure the teeth of crocodiles consist of hard, fine-tubed dentine, with an investing cap of enamel, and in addition a coating of cementum on their implanted portions. As already mentioned, they are implanted in tubular sockets, new successional teeth being continually developed at the inner side of their bases, and as the latter attain to a certain size, absorption attacks the base of the older tooth, and its successor moves into the space thus gained, so that it comes to be situated vertically beneath the older tooth. In its further growth it causes yet more absorption of the older tooth, which it ultimately pushes out in front of it, sometimes carrying the remains of the old tooth like a cap upon its own apex when it first emerges. Each new tooth vertically succeeds its predecessor; hence no additional teeth are added, but the young newly hatched crocodile has as many teeth as a full-grown one.

In the extinct *Ichthyosaurus* the teeth, while forming an armature not unlike that of some of the crocodiles, were not implanted in distinct sockets, but were lodged in a continuous shallow groove, with but slight indications of transverse divisions.

(iii.) **Lacertilia.**—The scaly reptiles, comprising the lizards and the snakes, run somewhat into one another.

The food varies from fruit and the like to insects, eggs, and small animals. The lizards have more or less conical teeth, though in some the cone is much flattened down and rounded. Again, the cone may be complicated by serrations or vertical ridges and prominences.

More rarely there are subsidiary cusps, generally set lengthwise, and there are but seldom inner or outer cusps which would bring it at all into the semblance of a mammalian tooth. The teeth are generally composed of a central body of hard dentine, more or less completely invested by a cap of enamel, and they are attached to the bone by anchylosis.

When the tooth is anchylosed by its outer side to an external parapet of bone, the creature is said to be "pleurodont"; when by the end of its base it is attached to the summit of a parapet, it is "acrodont."

The succession of teeth in most lizards is constant, new teeth being developed at the inner side of the bases of the old teeth, which become undermined by absorption, and fall off when the successional tooth has attained to a certain stage in its development.

The accompanying figure of the lower jaw of a Monitor lizard will give an idea of a dentition common in the group. The teeth are neither very large nor very numerous, there being about thirty in the jaw; towards the front of the mouth they are a little more pointed than at the back, but the differences in this respect are not striking.

At the inner side of the bases of the teeth are seen foramina which lead into the spaces in which new teeth are being developed.

Amongst the lizards considerable variety in the form of the teeth themselves exists, some having thin serrated edges, others being exceedingly blunt and rounded, but in the general disposition of the teeth there is considerable uniformity.

The teeth of some lizards consist at their apices of ordinary osteodentine, with a simple central pulp cavity, but at their bases of plici-dentine with numerous subdivisions of the pulp cavity, as is seen in the Monitor lizards (*Varanus*, see p. 91). One Mexican lizard (*Heloderma suspectum*) has the reputation of being poisonous, and has teeth which are grooved both back and front. Its harmful powers may have been exaggerated, but there is no doubt that the secretion is poisonous; indeed, the bite of a specimen in the Zoological Gardens has been found to be fatal to small animals, and Dr. Weir Mitchell states that in one instance it has been known to be fatal to man. It is, however, of gentle disposition, and not disposed to bite. The salivary glands of the lower jaw, probably the submaxillary glands, lie close against the under-side of the bone. In a dissection made by Professor Stewart upon a specimen in the College of Surgeons museum, there appear to be a number of ducts which seem to actually perforate the bone, and they emerge by a series of small holes which lie in the sulcus between the lip and the teeth, close to the necks of the teeth.

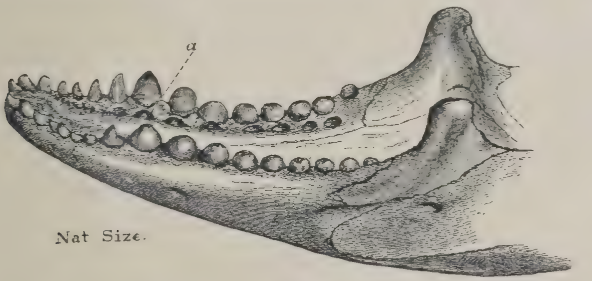

FIG. 175.—Lower jaw of a lizard (*Varanus gouldii*). *a*. Foramina leading to cavities of reserve.

In the *Python* the corresponding gland also has many ducts which open in a similar position, but they attain to it without any perforation of the bone, and there is no reason to suppose that their secretion is at all poisonous.

The teeth of the *Iguana* are somewhat slender, and the tops are flattened, lobed, and serrated. They are pleurodont, and the successional tooth moves sideways into the pulp cavity of its successor.

Although most reptiles have the teeth subequal in size, in the Agamoid group of lizards it is common to find tusk-like teeth in the canine region, and molariform teeth at the back.

In the common blindworm, which is zoologically a lizard which has lost its legs, the teeth are small and conical, like those of the snakes.

The chamæleons, which differ markedly in many respects from other lizards, are peculiar in having no replacement of their teeth, though, according to Röse (12), new teeth are constantly throughout life being added to the back of the series.

The absence of any succession of functional teeth is shared by another very peculiar lizard found in New Zealand, *Sphenodon*, the sole survivor of a very ancient and primitive group of reptiles, and it and its allies are now separated from the lizards and elevated into a separate order. Its very unusual dental armature was described by Günther (4), and has been subsequently reinvestigated by Spencer Harrison (5) and by Maggs and Payne (8). The premaxillary bones and the corresponding regions of the mandible each carry three teeth, which become fixed at their bases and are anchylosed to the bone. By wear they become knife-edged with a single notch, so that it used to be said that there were only two teeth in this situation, and their form recalls that of the gnawing incisors of rodents. There were originally fourteen other teeth on each side which are acrodont, and are imbedded for a short distance in the jaw. An inner row is carried upon the palatine bones, but the vomer is toothless, though Harrison describes vestigial teeth there also.

There is no functional replacement of teeth, so that when the teeth are worn down, as happens in old specimens, the actual sharp margins of the bone come into play as masticating organs. It occurred to the author as possible that these hard polished surfaces might have a coating of dentine upon them, but a microscopic examination which, by the kindness of Dr. Günther, he was enabled to make, proved that the dense ivory-like surface was true bone, and had no relation to dental structures.

With the exception of some fish, and there in a far more limited degree (cf. p. 272), there are few instances of actual bone being exposed and used for masticating purposes, though Harrison states that this happens in the true lizard, *Uromastyx*.

The tooth-band has been said to be continued beyond the germs of the functional teeth, although no successional teeth are formed, and Harrison has since described the existence of calcified embryonic teeth which never cut the gum.

Thus at an early age its dentition conforms more closely to that of its class, and it may be mentioned that its extinct allies do not all share its peculiarities, some having strongly developed teeth, as well as teeth on the vomer.

This animal presents an antero-posterior elongation of the condyle of the lower jaw, a character unique among reptiles.

(iv.) The **Ophidia,** or snakes, were formerly divided into two groups, the venomous and non-venomous snakes, but this division has been found to be unsatisfactory. They are, therefore, now usually grouped, with the exception of a few less important families allied to the first, into the pythons, the Colubrine snakes, and the Viperine snakes.

Another method of grouping the snakes is based entirely upon their teeth :

1. *Opoterodonta.* Teeth in one jaw only. Blind snakes.
2. *Aglypha.* Teeth in both jaws. None grooved.
3. *Opisthoglypha.* Posterior maxillary teeth grooved.
4. *Proteroglypha.* Anterior maxillary teeth grooved.
5. *Solenoglypha.* Anterior maxillary tooth isolated and perforated by a canal.

(These last two are often grouped together under the name *Proteroglypha.*)

In the small family of blind snakes the eye is rudimentary. Teeth may be present in the upper or in the lower jaw but not in both, and the mouth is incapable of wide opening. They are subterranean in their habits, and feed on larvæ, ants, &c.

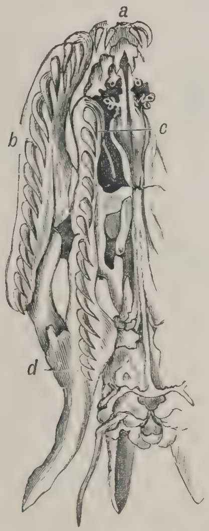

Fig. 176.—One half of the skull of a python (without the lower jaw) seen from below. *a.* Intermaxillary bone. *b.* Maxillary bone, carrying the outer row of teeth. *c, d.* Palatine and pterygoid bones, the teeth upon which constitute the inner or second row.

Of other snakes, the pythons are the least specialised in their characters, and may be described first. They have one row of teeth in the lower jaw, and two rows in the upper jaw. In the latter the maxillary bones carry one row, while a parallel internal row is supported upon the palatine and pterygoid bones.

The teeth are all strongly recurved, and firmly anchylosed to the bone. They consist of a central body of non-vascular dentine, coated by a very thin layer of enamel (there is not, as is generally supposed, any layer of cementum, the enamel having been erroneously supposed to be such).

The two halves of the lower jaw are connected at the symphysis by an exceedingly elastic ligament. Their articulation with the temporal bone is through the medium of an elongated movable quadrate bone, and is such as to allow of their being widely separated from the skull and from one another, which permits of the dilatation of the mouth rendered necessary by the large size of the creatures which a snake swallows.

The teeth of the snake are simply available for seizing prey and retaining it, as snakes invariably swallow their prey whole, and in no sense masticate it.

As the object to be swallowed is often so disproportionately large as to make the process of deglutition appear an impossibility, the mouth and pharynx have to undergo great dilatation.

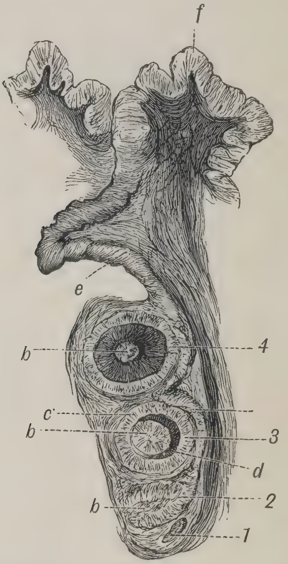

FIG. 177.—Developing teeth of a snake. *f*. Oral epithelium. *e*. Epithelium constituting the tooth-band. *b*. Dentine-pulp. *c*. Enamel cells. *d*. Dentine. 1, 2. Very young germs. 3, 4. Older germs.

The successional tooth-germs, which are very numerous, are also arranged in an unusual position, which by bringing them very close to the surface of the bone, to which they lie parallel, renders them less liable to displacement and injury than they would have been had they been placed vertically, as they are in all other creatures; while, in addition to the advantage of protection by position, they are wrapped round by a sort of adventitious capsule of connective tissue.

As the teeth during their development are thus lying down parallel with the length of the jaw-bone, when the period for replacing a predecessor arrives, they have not only to move upwards, but also to become erected; how this is done remains a mystery, for the author has been quite unable to discern the means by which it is accomplished.

When a snake has seized its food, which it retains by means of its many sharp recurved teeth, it slowly swallows it by advancing first its lower, then its upper, jaw, till it thus, so to speak, forces itself over the body of its prey. When this latter is large, deglutition is a very lengthy process, but an English snake can swallow a moderate-sized frog with considerable rapidity.

It has already been mentioned that many non-venomous snakes have two complete rows of teeth in the upper jaw, the outer row being situated on the maxillary bones, the inner upon the palatine and pterygoid bones. The teeth of such snakes as the pythons and boas are all simple recurved cones, without grooves or canals for the conveyance of a poisonous saliva, these snakes killing their prey by crushing it in the folds of their bodies.

The Colubrine snakes form a large group, of which some are harmless and others very poisonous; they comprise the *Aglypha*, *Opisthoglypha*, and the *Proteroglypha*.

Of the first group, or *Aglypha*, little need be said, as its typical members resemble in their dentition the pythons. They are all harmless, and our common English snake is one of them. Reduced dentitions occur, as in *Dasypeltis* (formerly called *Rachiodon*), an egg-eating snake which has no teeth in front of either jaw, and but very small ones behind. Its food consists of eggs, which thus escape breakage until they reach the œsophagus, into which processes from the under-surface of the vertebræ project, and there serve to break the egg. Snakes with their dentitions similarly modified exist also in India (*e.g.*, *Elachistodon*). The jaws are dilatable to an amazing extent, so that quite a small snake will get an unbroken hen's egg down into its throat.

The *Opisthoglypha* are not very numerous, but the Green Tree-snake and the Whip-snakes belong to this group. In them the hinder grooved maxillary teeth, which are either continuous with or separated by a blank interval from the solid teeth in front, are not more than twice the length of the latter. Sometimes a lower tooth is similarly modified. They are apparently not very poisonous, and some, perhaps, may not be so at all.

Alcock and Rogers (1) have made the interesting observation that an infusion of the parotid glands of some of the *Aglypha* and of the *Opisthoglypha* injected subcutaneously killed small mammals with symptoms like those of cobra poison. The serum of these snakes or an infusion of their Harderian glands (glands near the eye) were quite harmless, so that it would appear that the venomous nature of the salivary secretion in snakes is merely a question of degree.

With the *Proteroglypha* it is different, every one of the group being poisonous, though, it may be, with varying degrees of virulence. As in all the preceding snakes, the maxillary bone extends horizontally backwards and is fixed, but the front teeth upon it are more or less deeply grooved, this groove in some being so nearly closed in by its lips as to practically form a tube. The teeth which follow behind these poison fangs are usually reduced in number and solid. These poisonous snakes are characterised by a shortening of the series of teeth carried upon the maxillary bone, and by the front teeth of the series being developed to much greater length than those which lie behind it. Thus *Hydrophis*, a genus of poisonous sea snakes, has five or more teeth upon the maxillary bone, the foremost of which is much the largest, and this largest tooth is so deeply grooved upon its anterior surface as to be converted into a tube, the tube serving to convey the poison into the wounds inflicted by it.

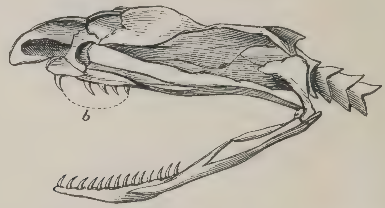

FIG. 178.—Head and jaws of *Hydrophis*. The maxillary bone (*b*), instead of carrying a complete series of teeth, is armed with a few teeth only near to the front. The foremost tooth is canaliculated, and forms the poison fang.

Enhydris has two grooved teeth, in which the groove is not closed, almost side by side at the front of each maxilla, the posterior being a little external. After an interspace five small solid teeth follow.

Hydrus has two grooved teeth, followed after an interval by seven or eight others.

Platurus has the maxilla very short and two grooved fangs, the grooves tightly closed, side by side on each maxilla (15).

Thus there is a gradation among these sea snakes leading towards the high specialisation of poison apparatus found in the Viperine group.

Although these Colubrine poisonous snakes are, so far as the elaboration of their poison apparatus goes, intermediate between the highly specialised Viperine snakes and the harmless ones, it must not be supposed that they are any the less dangerous in the quality of their poison. On the contrary, some of the most virulent, such as the cobra, are in this group, and the sea snakes just described are exceedingly deadly.

More recently it has been found by L. Rogers (12) that the poison of the water snakes (*Hydrophidæ*) is of most intense power, being from 5 to 20 times as powerful as cobra poison; for fishes it is 50 times as deadly. Thus the intensity of the poisonous nature of the parotid secretion in snakes which are so lethal as to be subscribed as "poisonous" stands in no close relation to the elaboration of the poison apparatus. Thus the cobra, the most destructive to human life, has upon the maxilla from one to three solid small teeth behind the poison fang, which is itself small.

The cobra has the maxilla still further shortened, reaching back only so far as the level of the orbit, and, its shortness being compensated by an increased length of the ectopterygoid, carries one or two rudimentary teeth behind the poison fang. The front of the maxilla is wide enough to give standing space to two fangs side by side, and the inner and outer positions are, in the succession of the fangs, occupied alternately; although now and again two fangs may be found complete and side by side, one of them is then usually loose. The poison fang is not more than a quarter or a third of an inch long, and fits in a depression in the lower lip, while the maxilla possesses some degree of mobility, so that the tooth at rest is not fully erect, but drops down through an angle of 40°, or less. The groove on the front of the fang is closed by the approximation of its lips, but these lips remain rounded, and are not flattened out against one another to form the completely fused joint seen in the Viperine snakes (Fig. 181).

The poison in all highly specialised poisonous snakes is secreted by a very large parotid gland, the duct of which ends close to the upper orifice of the canal of the fang, but does not enter it, the escape of the poison being to a great extent prevented by a kind of flap of mucous membrane, containing, according to West, muscular elements, which embraces the front of the tooth, especially when it is somewhat elevated. But the poison ejected by an angry cobra is far larger in amount than can all pass through the canal of the fang, so that it pours down all round it as well as through it. The cobra bites like a dog, whereas the Viperine snakes, though sometimes biting also, often merely strike with their much longer fangs (10).

The Australian death-adder and other poisonous snakes of that region all belong to the Colubrine group.

In the Viperine poisonous snakes (puff-adder, rattlesnake, vipers, &c.) the poison apparatus is yet more specialised. The maxillary bone carries no teeth at all behind the poison fang; it is so reduced in length as to be almost square in form, and is so articulated to the skull as to be freely movable.

The poison fang is of great length, so that if constantly erect it would be much in the way; when it is out of use, however, it is laid flat along the roof of the mouth, and is only erected for the purpose of striking. When in repose it is altogether hidden by a fold of mucous membrane, which, when the fang is erected, becomes tightly stretched over a part of its anterior surface, and serves to direct the poison down the poison canal and prevents, to a great extent, its escape around the exterior of the tooth.

The mechanism by which the poison fang is erected is thus described by Professor Huxley (6): "When the mouth is shut the axis of the quadrate bone is inclined downwards and backwards.

The pterygoid, thrown back as far as it can go, straightens the pterygo-palatine joint, and causes the axes of the palatine and pterygoid bones to coincide. The transverse bone, also carried back by the pterygoid, similarly pulls the posterior part of the maxilla and causes its proper palatine face, to which the great channelled poison fangs are attached, to look backwards. Hence these fangs lie along the roof of the mouth, concealed between folds of the mucous membrane. But when the animal opens its mouth for the purpose of striking its prey, the digastric muscles, pulling up the angle of the mandible, at the same time thrust the distal end of the quadrate bone forwards. This necessitates the pushing forward of the pterygoid, the result of which is twofold : firstly, the bending of the pterygo-palatine joint ; secondly, the partial rotation of the maxillary upon its lachrymal joint, the hidden edge of the maxillary being thrust downwards and forwards.

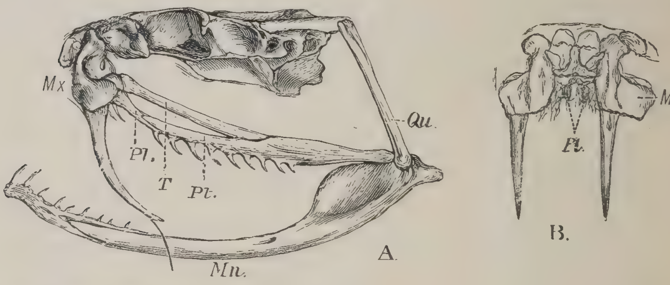

Fig. 179.—Side and front view of the skull of *Bothrops* (*Craspedocephalus*) *melas*, a large South American Viperine snake akin to the rattlesnakes. A bristle is passed down the poison canal. *Mx.* Maxillary bones. *Mn.* Mandible. *Pl.* Palatine bones. *Pt.* Pterygoid bones. *Qu.* Quadrate bone. *T.* Transverse bone.

A. Side view. B. Front view.

"In virtue of this rotation of the maxillary through about a quarter of a cycle, the dentigerous face of the maxilla looks downwards, and the fangs are erected into a vertical position. The snake 'strikes' by the simultaneous contraction of the crotaphite muscle, part of which extends over the poison gland, the poison is injected into the wound through the canal of the fang, and this being withdrawn, the mouth is shut, all the previous movements reversed, and the parts return to their first position."

The poison fang is a long, pointed, slightly recurved tooth, traversed by a canal which commences on its front surface, near to the bone, and terminates also on its front surface, a little distance short of its point ; in the figure a bristle has been passed through it, and shows the points where it commences and terminates (Fig. 179). This tube conveys the poison into the puncture, its upper orifice being in close relation with the end of the duct of the poison gland.

As may have been gathered from what has already been said, in Colubrine poisonous snakes the canal is more or less visible on the exterior of the tooth, where an apparent fissure marks the point where the two lips of the groove have met. Thus the poison fang of *Hydrophis*, although through a part of its length the canal is quite closed in, has a very marked line along its anterior surface, and in section it looks much as would the dentine in Fig. 180, if the two cornua had their rounded extremities brought together into actual contact, without, however, their rounded outlines being altered.

By imagining an anterior groove to be deepened, and finally converted into a canal by its edges growing up and meeting over it, we shall have a fair conception of the nature of the tube in a poison fang, which is thus really outside the tooth. It might thus, at least in its canaliculated part, be regarded as a thin flattened tooth bent round so as to form a tube. Just as there are gradations in the armature of the maxillary bone, which link together the extreme forms of the harmless python and the venomous rattlesnake, so there are gradations in the form of the grooving and the completeness of the canal between the Colubrine and Viperine poisonous snakes.

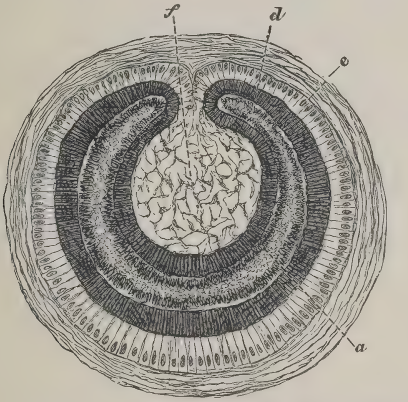

Fig. 180.—Transverse section of tooth-sac of poison fang of viper prior to the complete closure of the poison tube by the meeting together of the two cornua of the dentine. *a*. Dental pulp. *d*. Dentine. *e*. Ameloblasts of cellular tissue which ultimately disappear.

But in the poison fang of a Viperine snake the lips of the groove are flattened and fitted to one another, so that not a vestige of the join can be seen upon the smooth exterior of the tooth. In the following figure (Fig. 181) the pulp cavity is seen to be a thin flattened chamber partly surrounding the tube formed for the conveyance of the poison.

The poison fang is exceedingly sharp, its point being continued some little distance beyond the place where the poison canal opens on the front of the tooth. This disposition of parts has been copied in the points of syringes for making subcutaneous injections.

The dentine is continued down to a very fine point, and it is cased by an exceedingly thin layer of enamel, not much more than $\frac{1}{600}$ of an inch in thickness in our common English viper; thus the utmost sharpness is secured, without loss of elasticity, which would have ensued had its point been made up of brittle enamel only. Enamel covers the whole exterior of the tooth, but does not extend into the poison canal in the Viperine snakes, but in *Hydrophis* probably this is the case. As the point is simple, the tooth-germ of a poison fang only becomes distinguishable from that of any other ophidian tooth after the tip has been formed, when a groove appears on its side. (See 8 and 9 in Fig. 182.)

The large size of the canal in the Viperine snakes enables them to send a jet of poison through it, whereas only a drop can be forced through the small canal of a cobra.

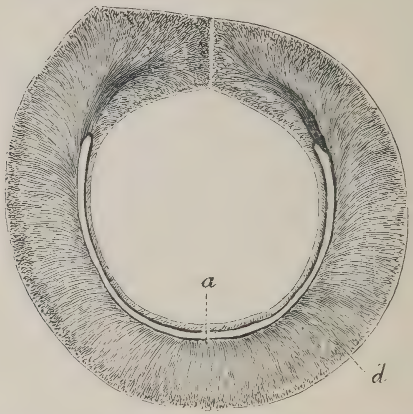

FIG. 181.—Transverse section of the poison fang of a rattlesnake. *a*. Pulp cavity. *d*. Dentine.

It being the habit of poisonous snakes to make use of these weapons to kill their prey, which they consequently do not swallow alive, it would obviously subject them to no little inconvenience to be without these weapons for any considerable length of time, while from their habit of striking living prey the long fangs must be very liable to be broken off by the jumping away of the creature struck, to say nothing of the great force with which the blow is given.

In the most typical (Viperine) poisonous snakes the succession of teeth is conducted upon a plan which is unique, and which is excellently adapted to save loss of time in the replacement of a lost poison fang. Upon the movable maxillary bones there is space enough for two poison fangs, side by side; only one, however, is fully anchylosed to the bone at a time, and occupies a place to the extreme right or extreme left of the bone, as the case may be, leaving vacant space for another by its side.

When the tooth in use falls, it will be succeeded by a tooth upon the vacant spot by its side, not upon the spot upon which itself stood, so that the places on the right and the left of the bone are occupied alternately by the tooth in use. Thus, in Fig. 179, the poison fang of the snake's right side is seen occupying a position on the extreme outside of the maxillary bone, while its left poison fang is fixed on the inside of the maxillary bone.

The upper boundary of Fig. 182 is formed by the flap of mucous membrane which covers in the poison fang when at rest. Nos. 1 and 2 lie in the pouch formed by it, the section happening to be taken from a specimen in which the tooth was about to be changed. In most specimens one tooth only, the tooth actually in use, is seen in this position.

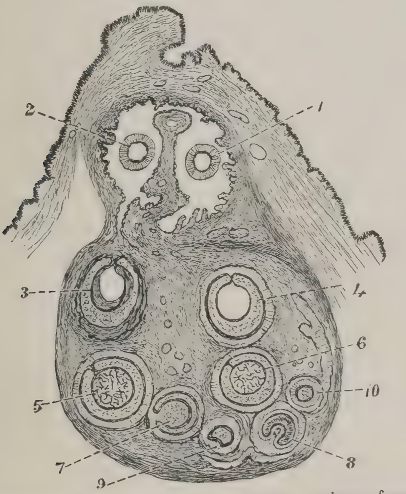

Fig. 182.—Transverse sections of the reserve poison fangs of a viper. 1. Tooth at present in use in its recumbent position; were it erect it would be withdrawn from view, or else seen in longitudinal section. 2. Tooth which will next succeed to No. 1. 3, 4, 5, &c. Tooth-sacs numbered in the order in which they will succeed.

A flap hanging freely across this space serves apparently to keep teeth of the one series from getting over to the other side, and probably serves to hold in place the reserve tooth when the older tooth is erected for biting.

The reserve poison fangs, as many as ten in number in the rattlesnake, are likewise arranged in two parallel series, in which the teeth exist in pairs of almost equal age. The tooth in use is thus derived alternately from the one and the other series, as is indicated by the consecutive numbers of the figure, a septum of connective tissue keeping the two series of teeth distinct from one another.

The teeth being arranged in pairs of almost equal age, suggest that the succession is both rapid and regular. All the reserve teeth lie recumbent in and behind the sheath of mucous membrane which covers in the functional tooth.

This arrangement of the successional teeth in a paired series does not exist in the cobra, in which the successional teeth form but a single series. Perhaps this may serve to explain the preference of the snake-charmers for the cobra, which would probably take longer to replace a removed poison fang than would a Viperine snake.*

But in the Colubrine venomous snakes (cf. p. 288) the successional poison fang sometimes makes its way to a spot to the side of its predecessor, so that there may possibly be no loss of time; and notwithstanding that they are in a measure transitional forms between the harmless and the Viperine snakes, some of them are most virulently poisonous and deadly in their bite.†

This arrangement of *two* distinct chains of younger developing organs, all destined to keep the creature always supplied with *one* organ in a state of efficiency, is, so far as I know, without parallel.

A clue to the nature of the arrangement seems, however, to be afforded by some of the Colubrine poisonous sea snakes (cf. p. 289), in which it was found by West that in some forms which retain more than one large tooth upon the maxilla the second tooth had moved forwards till it stood nearly or quite at the side of the first, and something of the same kind was noted in the cobra.

It would seem, then, that the Viperine snake has really retained two of its maxillary teeth, although, their development alternating, it has only one in use at a time; and that the second tooth and its chain of successors have come to be arranged in pairs with the first tooth and its successors, thus explaining an otherwise very anomalous arrangement.

Like other ophidian teeth, the poison fangs become anchylosed to the bone which carries them, their secure fixation being aided by the base of the tooth being fluted, as well as by a sort of buttress work of new bone, being thrown out to secure each new poison fang as it comes into place.

L. Kathariner (⁷) has investigated the development of poison fangs in the viper, and holds that the two series arise from but one tooth band, a view also held by Röse. If this be true, it renders less probable the suggestion made in the text that the functional teeth represent not one, but really two, of the once numerous maxillary teeth. However, Voerckel (¹⁴) holds that there are two separate tooth bands, a conclusion which seems *à priori* much more probable.

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* An inquiry inserted in an Indian newspaper elicited the following answer :—"I have frequently seen snake-charmers exhibit snakes of the family *Viperidæ*, chiefly the *Daboia russelli* and *Echis carinata*. I have also been told by some snake-charmers that they considered the *Daboia* even more poisonous than the cobra; and judging from the cautious way in which they handle these snakes—never lifting them off the ground without first putting a stick on their necks to hold them down—I feel pretty sure they all consider the vipers more dangerous than the cobras."

† A more detailed account of the succession of poison fangs has been given in the "Philos. Trans.," 1876, Part I.

Kathariner gives a valuable description of the means by which each new tooth comes into close relation with the poison ducts, and holds, amongst other points, that the originally solid epithelial rudiment of the poison ducts sends extensions down to each series of tooth-germs, and that the successional teeth travel along this opened-up track to their places.

He denies the existence of enamel on these teeth, affirms that of an enamel cuticle, and states that there is not only cementum (which term he prefers to the author's "bone of attachment"), but also a modified dentine, which he styles fibro-dentine intervening between the ordinary dentine and the cementum.

[As has been stated above, the teeth of most reptiles undergo constant successional replacement throughout life; they are in fact polyphyodont, each individual tooth of a series being replaced by its morphological successor, developed as an outgrowth of the dental lamina in the same situation. Bolk has, however, given an entirely different conception of this arrangement and succession of the teeth in reptiles (^{2a}), and in doing so has introduced a new and somewhat awe-inspiring terminology. The teeth of the reptiles have hitherto been regarded as belonging to one and the self-same row, a condition termed by Bolk as *monostichical*. In his opinion this is incorrect, the reptilian dentition, like the mammalian, being *distichical*, that is to say that the teeth, though standing in a single row, must be regarded as belonging to two rows, the individual teeth of which have secondarily become interpolated alternately between each other; they are not, therefore, replacing teeth in the true sense of the word. Furthermore, Bolk thinks that the dental system must have been originally *tristichical*, the outer row having become rudimentary, though aborted representatives may still be present in some of the living reptiles. These last are termed the *parastichos*, the middle and inner of the three parallel rows the *exostichos* and *endostichos* respectively.

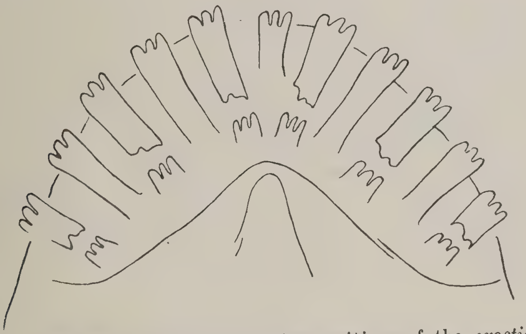

FIG. 183.—Diagram showing the relative positions of the *exostichos* and *endostichos* in *Tupinambus nigropunctatus*. (After Bolk, Koninklijke Akad. van Wetenschappen te Amsterdam, February, 1912.)

The diagrams here inserted (Figs. 183, 184) have been taken from

Bolk's paper and will render his idea sufficiently intelligible ; but for the full details and for the evidence upon which his belief is based the reader is referred to the original paper.

This interpretation of Bolk's closely approximates to the description of the method of tooth succession in the Viperine snakes, and which is stated by the author to be unique, but which, in the opinion of Bolk, is the rule. A very full account of the development and succession of the teeth of reptiles has been given by Woedeman (16), who confirms the conclusions arrived at by Bolk.]

Dinosauria.—Some of these huge extinct creatures, which flourished during the secondary period, when the mammals were but feebly represented, attained a length of sixty feet or thereabouts, though there were also some small forms. They present affinities with the crocodiles and were also in some respects bird-like, the great iguanodons, of which some fine examples are to be seen in the Brussels Museum, sitting up on their hind legs and tails, and having but short front legs. These Dinosaurs had a distinct chin bone and a contour of the front of the jaws more or less sharp and beak-shaped, and devoid of teeth.

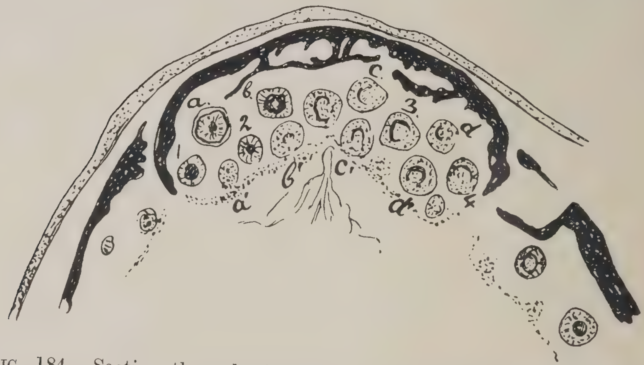

FIG. 184.—Section through the jaw of *Lygosoma olivaceum* (somewhat slanting). The letters represent the *exostichos*, the numerals the *endostichos*. In the median line are unpaired teeth. The endostichos are seen to be alternating and not replacing teeth. (After Bolk, Koninklijke Akad. van Wetenschappen te Amsterdam, February, 1912.)

The teeth were not implanted in distinct sockets, and in many of the group had expanded and flattened crowns like those of the iguana, whence the name iguanodon, but it must not be supposed that they therefore had any particular affinity with that lizard. In them the outer alveolar wall was considerably higher than the inner, and the transverse septa not very complete. The roots of the teeth were more or less perfectly cylindrical, and the enamelled crowns compressed and expanded, with trenchant edges. The tooth of the iguanodon will serve as a fair example of a Dinosaurian tooth. The crown is greatly expanded, and presents anterior and posterior sharp-notched margins; the enamel is laid over the outer surface of upper teeth, and the inner of lower teeth. The enamelled surface is ridged, so that as it wears down a notched edge is maintained. Moreover, the maintenance of a sharp edge is further secured by the dentine on the enamelled side of the crown being of the hard unvascular variety, that on the inner being vaso-dentine and therefore softer. The remnant of the pulp ossifies, and comes into use, as these teeth remained at work until worn quite to a flat surface. The root portion was smooth, round, and curved.

Professor Marsh (9) has described and figured a peculiar Dinosaurian dentition in a reptile to which he gave the name of *Stegosaurus*. The teeth are slightly compressed transversely and are covered with a thin enamel; the roots are long and slender, implanted weakly in separate sockets. But at the inner side of the root of the tooth in use were no less than five successional teeth, in graduated stages of development, ready to ultimately take its place; so large a number of successional teeth has not hitherto been met with in a Dinosaur.

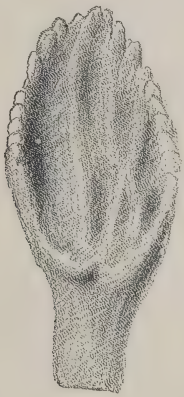

Fig. 185.—Tooth of *Iguanodon*. (After Owen.)

Anomodont Reptiles.—This reptilian order, established many years ago by the late Sir Richard Owen, contains a considerable number of forms which, so far as their teeth are concerned, are somewhat divergent, the order being formed upon various characters of the skull and skeleton.

The original fossils came from South Africa, whence a large number have since been obtained, but others have been found in Europe and America, also in deposits of the Triassic and Permian periods.

They have been investigated by the late Professor Huxley, Professor Cope, and many others, but the most complete account is to be found in a series of elaborate papers by Professor Seeley, published in the "Philos. Trans.," 1888—1895.*

By the last-named writer they are divided into two sub-orders, the *Therochelonia* and the *Therosuchia*, each of which is of the greatest interest to the odontologist, the former because they present such a highly aberrant dentition, and the latter because of the close general resemblance which the teeth in some members of the group present to those of mammals.

Of the *Therochelonia*, so styled on account of resemblances in the palate to that of *Chelonia*, the genus *Dicynodon* of Owen is best known.

In it the only teeth known are two exceedingly long and strong tusks which project down from the upper jaw in the position where canine teeth usually occur. The extent to which the tusks are developed varies considerably in different species, and even in the two sexes of the same species. One specimen at the British Museum of what seems to be *Dicynodon microtrema* has a number of small molars. It is not known how far some of the specimens with small molars, such as *Prodicynodon*, *Diœlurodon* or *Pristerodon*, may possibly be young *Dicynodons* (³). The margin of the toothless mandible was rather sharp, just as in turtles and tortoises, and was,

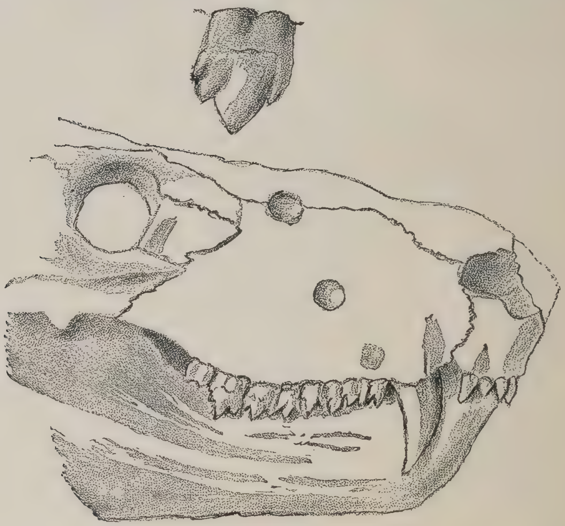

Fig. 186.—Dentition of *Cynognathus* (after Seeley), with single upper tooth on large scale; quarter natural size.

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* Our knowledge of the fossil reptiles of South Africa has been greatly extended during the past few years by the admirable researches of Dr. R. Broom, and of the palæontology of the reptiles in general by those of Professor D. M. S. Watson, F.R.S.—H. W. M. T.

perhaps, covered with a horny bill, as may also have been the maxilla.

Seeley points out that the tusk is not truly a canine because it is implanted some distance behind the premaxillary suture, but this is not of much importance, since, for reasons given on a succeeding page, the canine can no longer be regarded as a morphological entity, and we may hence apply the term to any caniniform tooth ; and, as it is implanted in a socket considerably produced, it may easily have commenced its development close to the suture.

The other group, the *Therosuchia*, present dentitions very varied in character, some (*Procolophon*) have conical, cylindrical teeth of sub-equal size, with expanded bases in close union with the jaw, and teeth upon the palate ; the teeth of the upper and lower jaws interdigitate, and all the usual characters of a reptilian dentition are present.

But the main interest lies in the sub-group, the Theriodontia, where for the first time we meet with teeth which may be divided into incisors, canines, and molars, and in which the general appearance of the dentition is distinctly mammalian, *i.e.*, heterodont. Nevertheless the composite lower jaw remains, in the distinctness of its component bones, thoroughly reptilian, and the molars show in different forms many gradations between the simple reptilian cones (*Ælurosaurus*) and the tuberculated many-cusped teeth (*Diademodon*).

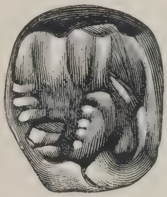

FIG. 187.—M_3 of *Diademodon* × 4. (After Seeley.)

A general idea of these dentitions may be gained from the genus *Cynognathus* here figured. The incisors stand in a rounded curve, and have slightly serrated margins ; there are four in each of the premaxillæ, and in the lower jaw there are probably three on each side, the outermost being the largest, as in carnivora.

There is a diastema in front of the large upper caniniform tooth, while the corresponding tooth in the lower jaw passes up inside it, being received into a deep fossa. Behind this tooth follow nine others which, on account of the greater simplicity of the first five, may be divided into five premolars and four molars.

The molars have a principal cusp and several subsidiary cusps. The enamel terminates in a distinct margin, and there is a slight hint of a division into two roots ; there are, however, no internal cusps, and the upper and lower molars work upon one another with a shearing action.

A point of great interest is that there is an indication of a cingulum, which in other forms, *e.g.*, *Nythosaurus*, is well marked. The advocates of the tritubercular theory place the cingulum in a very unimportant position, explaining the genesis of tooth cusps in quite other ways, whereas those who do not accept this theory in its entirety attribute to the cingulum a much more important *rôle* as the source of additional cusps.

If, then, the Theriodonts lie upon, or close to, the direct line of mammalian ancestry, as most zoologists consider that they do, the appearance of the cingulum at so early a period seems significant, for here, according to the one school, are additional cusps *in posse*.

In number the teeth vary considerably; some had as many as six incisors on each side of the upper jaw (*Pristerognathus*), while others (*Deuterosaurus*) had the molars reduced to one on each side. Two-rooted teeth, not otherwise known amongst reptilia, appear in *Tritylodon*. But the molars in some attain to a much higher degree of differentiation, so that Seeley writes of *Diademodon* that "if its teeth had occurred isolated it would have been legitimate to have referred them to mammals."

The molar teeth are of quadrate form, with two or three cusps on the anterior border, one tubercle on the anterior and several on the posterior border; there is also a tubercle in the middle of the crown. They are usually single-rooted, and often show much attrition. The premolars were small, the canine large and fluted; the incisors are unknown. The premolars were generally small, circular, and tuberculate, but in some allied forms they were laterally compressed.

Some of these reptiles attained to considerable size; thus, Sir Richard Owen (11) described, under the name of *Cynodraco*, one as large as a lion, which had eight incisors in the lower jaw, of which the first is the smallest, and a canine of moderate size. The upper incisors are not known, but there were a pair of upper canines of such size that they extended down along the outside of a flattened portion of the lower jaw, like the canine teeth of *Machairodus* and those of *Dinoceras*. This protection of an especially long upper tooth by a corresponding downgrowth of the lower jaw is by no means an unusual provision of nature. Besides being met with in the instances cited, it is seen in *Tinoceras*, another of the Dinocerata, and in *Chauliodus*, a deep-sea fish dredged up by the *Challenger*. It is, however, not a universal structure, as it is quite absent in the musk deer. The hinder margins of these canines were trenchant and finely serrated. The molar teeth are not known.

In the Anomodontia there is no evidence of a replacement of the canine, but in genera with numerous small molars, *e.g.*, *Diœlurodon*, *Prodicynodon* and others, there is evidence of an indefinite replacement of the molars. Recently (3b) Broom has discovered evidence of a mammal-like dental succession in the Cynodont reptiles, while in the Therocephalia dental replacement has long been known in the incisors and canines.

A genus to which the name *Anomodon* has been given had nothing but two tusks in the upper jaw, the lower being wholly edentulous, and the Placodontia had incisor-like teeth in front, with rounded, flattish teeth at the back, the palate being furnished with similar teeth, quite unlike those of any other reptile.

It has been mentioned that the lower jaw consists of all the usual components of the reptilian jaw, but the dentary bone forms so large a proportion of the whole, that it is suggested that this is the chief element in the mammalian jaw.

The **Pterosauria,** or flying reptiles, have, since the discovery of toothed birds, become of special interest to the odontologist. The wings were stretched membranes, like those of a bat, and the measurement across their tips in some of the largest must have been twenty-five feet ; but most of those known were much smaller, from ten to fifteen inches in total length of body. In the Pterodactyls the jaws are furnished with long, slender, sharp teeth in their whole length ; but in *Ramphorhynchus* the anterior extremities of the jaws are without teeth, and it has been conjectured that these portions were sheathed in horny beaks.

And Professor Marsh (9) has discovered, in the same formation in which he found the toothed birds, several species of Pterodactyls wholly without teeth, for which the generic name *Pteranodon* is proposed.

Its jaws, which are more like those of birds than those of any known reptile, show no traces of teeth, and the premaxillaries seem to have been encased in a horny covering.

THE TEETH OF BIRDS.

Prior to the discovery by Marsh, in 1870, of the remains of birds with teeth in the cretaceous formations of Western Kansas, little was with certainty known about the existence of teeth in any bird, although one or two fossils, leading to the suspicion that birds might have possessed teeth, were known. The state of knowledge up to that time has been clearly summarised by Woodward (17) to this effect : that it had been long supposed that no examples of teeth were to be met with amongst the birds, although some, such as the *Merganser*, have the margins of the bill serrated, so that the functions of teeth are discharged by this horny armature of the jaws.

The point of the bill is hooked, and for a little way behind the point is smooth, the corresponding part of the lower bill being also smooth. The lower bill is furnished with one row of pointed horny teeth, which fit in between two rows on the upper bill, the latter raking backwards.

They are apparently horny, near the apices there are some fine canals, and each is seated upon a vascular papilla ; their bases coalesce, so that there is a continuous horny sheath to the jaw.

It has been said that bony prominences correspond to these so called teeth, but in the specimen examined by the author no trace of such a thing could be seen.

In the fossil bird described by Professor Owen, from the London clay, under the name of *Odontopteryx toliapicus*, the form of the bill is not known, but the margins of the jaws are furnished with strong bony prominences. Geoffroy St. Hilaire had described a series of vascular pulps as existing on the margin of the jaw of parroquets just about to be hatched, which, though destined to form a horny bill, and not to be calcified into teeth, yet strikingly recall dental pulps. Then there is also the famous fossil *Archæopteryx*, an anomalous, oölitic bird, with a long and jointed tail, which possessed teeth. In the first specimen described there was a flaw in the evidence, inasmuch as the toothed jaw was not *in situ*, and so possibly might have belonged to another creature; but in the specimen now at Berlin there can be no question.

In successive expeditions, conducted under great difficulties owing to the extremes of heat and cold, and to the hostility of the Indians, the remains of no fewer than one hundred and fifty different individuals referable to the sub-class ODONTORNITHES have been obtained by Professor Marsh; they are classified under nine genera and twenty species.

They are referable to two widely different types, one group consisting of comparatively small birds, with great power of flight, and having their teeth implanted in distinct sockets (*Odontotornæ*, illustrated by the genus *Ichthyornis* as a type), the other group consisting of very large swimming birds without wings, and having teeth in grooves (*Odontolcæ*, type genus *Hesperornis*).

In *Ichthyornis* the teeth were about twenty-one in number in each ramus, all sharp and pointed, and recurved; the crowns were coated with enamel, and the front and back edges sharp but not serrated.

They are implanted in distinct though shallow sockets, and the maxillary teeth are a little larger than those opposing them; the premaxillaries were probably edentulous, and perhaps covered with a horny bill.

In the lower jaw the largest teeth occur about the middle of the ramus, those at its posterior end being materially smaller; and the sockets are deeper and stronger than in the upper jaw. The succession takes place vertically, as in crocodiles and dinosaurs.

The genus *Hesperornis*, probably diving birds, includes species six feet in length. As has already been mentioned, the teeth are not implanted in distinct sockets, but lie in a continuous groove like those of *Ichthyosaurus*. Slight projections from the lateral walls indicate a partitioning off into sockets, but nothing more than this is attained, and after the perishing of the soft parts the teeth were easily displaced, and had often fallen out of the jaws. The premaxillary bone is edentulous, but the teeth extend quite to the anterior extremity of the lower jaw. In one specimen there are fourteen sockets in the maxillary bone, and thirty-three in the corresponding lower ramus.

The successional tooth-germs were formed at the side of the base of the old ones, and, causing absorption of the old roots, migrated into the excavations so formed, grew large, and ultimately expelled their predecessors, as is seen in the accompanying figure.

In structure these teeth consist of hard dentine, invested with a rather thin layer of enamel, and having a large axial pulp cavity. The basal portion of the roots consists of osteo-dentine.

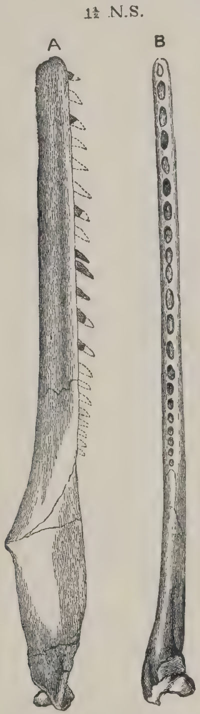

Fig. 188.—Mandible of *Ichthyornis*. (After Professor Marsh.) A. Side view, showing the teeth *in situ*. B. View of upper surface, showing the sockets in which the teeth were implanted.

The outer side of the crown is nearly flat, the inner strongly convex: the junction of these surfaces is marked by a sharp ridge, not serrated; and in addition the teeth are curved backwards, so that the anterior surface is convex and the posterior concave.

In form the teeth of *Hesperornis* present a close resemblance to those of *Mosasaurus*, a great extinct lizard.

Indeed, as Marsh observes, " in all their main features the teeth of

Hesperornis are essentially reptilian, and no anatomist would hesitate to refer them to that class had they been found alone. Combined with the other reptilian characters of *Hesperornis*, . . . they clearly indicate a genetic connection with that group."

In the dentine, contour lines are abundant ; the enamel is so dense as to appear structureless, and there is no coronal cementum.

The foregoing account is condensed from the magnificent volume published by the United States Government Geological Exploration (" Odontornithes : a Monograph," &c., by O. C. Marsh, Professor of Palæontology, Yale College).

With these notable exceptions, the jaws of all known birds are toothless, the horny cases forming their beaks taking the places and fulfilling the functions of teeth.

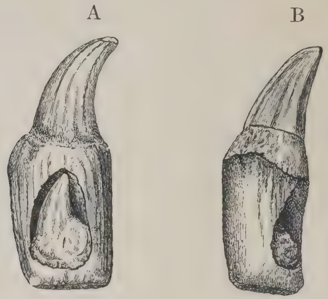

Fig. 189.—(After Professor Marsh.) A. *Hesperornis regalis*, with successional tooth in an excavation at its base ; enlarged eight diameters. B. Tooth of *Mosasaurus princeps*, half natural size, seen nearly in profile.

It would therefore seem possible that the ancestral birds all had true teeth, and it is possible that a sufficiently extended search might reveal rudimentary teeth surviving beneath the functional horny bill, or even possibly above it, like those of *Ornithorhynchus*. Indeed, Röse has found that in *Sterna* the tooth band exists, though no rudiments are to be found of more differentiated tooth-germs, though, judging from his figures, some might doubt the propriety of identifying so small an inflection of epithelium as being with any certainty a rudimentary tooth-band.

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CHAPTER XII.

HOMOLOGIES OF THE MAMMALIAN TEETH.

ALTHOUGH it is generally believed that the ancestors of the mammals are to be sought amongst the reptiles, and some of these, as we have seen (p. 299), had attained to a differentiation between the teeth in different parts of the mouth, such differentiation is not universal amongst them. There are some mammalian orders in which the teeth are alike in all parts of the mouth, and are of simple form, usually simple cones; it also happens that this simplicity of form frequently goes hand in hand with the absence of any functional succession in the teeth. Hence homodont and monophyodont * are terms often applicable to the same creatures. Of homodont mammals, *i.e.*, those which have similar teeth in all parts of the jaws, certain of the Cetacea afford good examples. Thus the dolphin (Fig. 190) has a great number of sharp conical teeth, those of the lower jaw alternating with and fitting in between those of the upper jaw, and it is by some believed that the teeth of higher mammals are derived from some such type of dentition, though not from these particular ones, for the Cetacea do not stand in the line of descent, but have retrograded so far as their teeth are concerned.

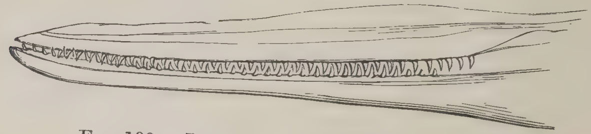

FIG. 190.—Jaws of common dolphin (homodont).

But it is far more common for the teeth in different regions of the mouth to present material differences of form, and such dentitions are termed heterŏdont. Those animals having a heterodont dentition are possessed of two sets of teeth, a milk and a permanent, *i.e.*, diphyodont.

A superficial survey of the teeth of those mammals which possess two sets of teeth (heterodont diphyodonts) will indicate that, notwithstanding the apparent anomalies brought about by adaptive modifications, a correspondence exists between the several teeth of different animals. That is to say, we can generally identify incisors, premolars, and molars. Nay, more, when an animal has less than the full typical number of a particular class of teeth, we can ordinarily say with some degree of certainty which of them it is that are absent.

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* The term monophyodont was originally introduced by Owen to signify animals with a single set of teeth. At that time dried skulls only had been examined. With the application of histological methods it was found that in most cases, hitherto regarded as truly monophyodont, functionless representatives of other dentitions were to be found. Strictly speaking, therefore, there are but very few monophyodont mammals. The term may, however, be conveniently retained in the more limited sense of animals with a single *functional* dentition, such, for example, as the toothed whales.—H. W. M. T.

Teeth are divided into incisors, canines, premolars, and molars, but these classes, though convenient, do not all admit of quite satisfactory definition. Incisors are defined as teeth implanted in the premaxillary bone, a definition which has the merit of being precise; while on the whole there is a certain resemblance running through incisor teeth in most mammals. But the definition of lower incisors as being the corresponding teeth in the lower jaw is a good deal less satisfactory, because they are not situated upon any distinct bone. It has even been denied that there can be a true homology between a maxillary and a mandibular tooth.

Incisors usually have but a single root, but in *Galeopithecus* (erroneously called a flying lemur) the outermost of the upper incisors are implanted by two roots, as is also the canine, which does not differ in any marked degree from the incisors.

Molars are teeth at the back of the mouth, which have no functional milk predecessors. They are generally subservient to grinding the food.

Premolars are teeth situated, in the case of the upper jaw, in the maxillary bone and in front of the molars, usually differing from them by being smaller and more simple in form, and, in typical diphyodonts, by having displaced deciduous predecessors.* But they are not always simpler in form, nor smaller (*e.g.*, in the horse), nor do they always displace deciduous predecessors (*e.g.*, they do not all do so in the marsupials, and the first premolar but rarely displaces a deciduous predecessor in other mammalia), so that this definition is not absolutely precise. Molars and premolars are often grouped together under the term "cheek teeth," and one palæontologist, Ameghino (²), abandoned the distinction between premolars and molars, and has numbered the teeth behind the canine continuously from one to seven.

Any objection that can be raised to the name of premolar on the score of a short strictly logical definition being impossible applies with tenfold force to the canines (⁶).

The nearest approach to a good definition is that which describes the canine as the tooth implanted in or immediately behind the premaxillo-maxillary suture, provided it be not far behind it, and the

* The classical definition of premolars and molars as being cheek teeth with or without predecessors respectively entirely fails when non-erupted teeth are taken into account. Numerous investigators have found evidences of vestigial teeth to the outer side of the so-called molars. Though difficult to eradicate the old nomenclature, the term "cheek teeth" is undoubtedly preferable. Though it is possible in most cases to distinguish the premolars from the molars by their crown patterns, it is impossible in other cases to do so.—H. W. M. T.

lower canine as the tooth which closes in front of the upper canine.

A great deal of confusion has arisen out of the twofold sense in which the word " canine " is used. If it were always applied to the first tooth in the maxilla of the typical mammalian dentition, quite irrespective of its size, &c., and to the lower tooth closing in front of it, no objection to its employment could be made, inasmuch as it would designate truly homologous organs.

But it so happens that the tooth in question is, in a number of familiar animals, developed to a large size and sharply pointed for use as a weapon, and so with the word canine there comes to be associated a teleological idea, and we come to be dissatisfied with calling the first maxillary tooth " canine," when there is some other tooth which is doing its special sort of work.

On the other hand, if we are to leave out of court all considerations as to size, purpose to which it is to be applied, and so forth, there is nothing left to make it deserving of a name distinguishing it from the four premolar teeth behind it. So we must be content with some such statement as the following :—

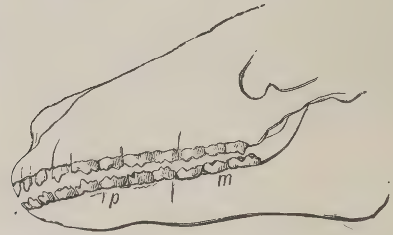

FIG. 191.—Side view of the dentition of *Anoplotherium*. (After Owen.)
p = premolars. m = molar teeth.

A large number of animals, notably the carnivora, have one tooth, situated a little way from the front of the mouth, developed to an unusual length and sharply pointed for use as a weapon. The tooth which has undergone this adaptive modification is usually the first which lies in the maxillary bone, in fact, the foremost of the premolar series ; but it occasionally happens that it is some other tooth which has undergone this modification. When the term canine is used it should generally mean a tooth so modified, and generally, but not always, should be alluding to the same tooth, *i.e.*, to the tooth which in the typical mammalian dentition comes next behind the outermost incisor—the first of the premolars, if we count five premolars instead of four.

It would obviously be very inconvenient to abolish the term canine, and some naturalists will continue to call the tooth which fulfils the function " canine," whilst others will apply the term to the homologous tooth, whatever be its shape. But it should be borne in mind that its significance is merely equivalent to "caniniform premolar," and thus that in describing the dog's dentition we should be accurate were we to say that it has five premolars, of which the first is caniniform. To those who accept the doctrine of evolution it is not needful to say more, as it is hardly possible to resist the conclusion that the teeth of the parent forms were, like those of the present monophyodonts, not much differentiated from one another, as is exemplified by the actual ungulate *Anoplotherium*. Then, as animals diverged and became modified in accordance with their requirements, their teeth would become so far differentiated that they would admit of being classified. Thus the carnivora would have attained to a stage of differentiation in which the canine is, functionally, certainly deserving of a distinction, whereas along other lines of descent, differentiation having not proceeded so far, or having proceeded in a somewhat different direction, it would not merit a distinctive appellation.

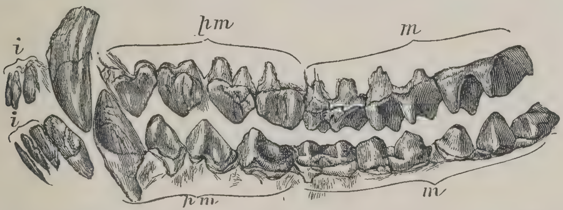

Fig. 192.—*Oreodon culbertsonii*. (After Leidy.) It will be observed that in the upper jaw the four premolars of the typical mammalian dentition are behind the "canine," but that in the lower jaw the tooth which would fulfil the functions of a canine is the first of these four, and therefore is *not* the corresponding tooth to the "canine" in the upper jaw.

It may be desirable to point out a few instances of the difficulties to which those anatomists are committed who call some tooth a "canine" in every case where a tooth is situated in the maxillary bone, close behind the suture which connects it with the intermaxillary bone, whether that or any other tooth be large and pointed, "caniniform" or not.

In typical ruminants, the upper jaw lacks both incisors and canines (with certain exceptions), but in front of the lower jaw there are grouped together eight teeth, closely fitted to one another, and of almost exactly similar size and shape. The outermost pair of these teeth are called canines, because (i.) in some allied species the tooth in this situation is more pointed; (ii.) because this tooth shuts in advance of the upper canine when the mouth is closed in those allied creatures which have an undoubted upper canine; (iii.) because it is cut later than the others (Owen); (iv.) because six is the typical number of mammalian incisors.

The first three reasons are weak, because form (i.) is a very unsafe guide to homology, and as to the lateness of its development (iii.), it succeeds to the third incisor, by Professor Owen's own showing, after about the same lapse of time which separated the eruption of the second and third incisors.

Oreodon, an extinct ruminant with caniniform teeth, has the eight incisors in the lower jaw in addition to a caniniform tooth, which is the fifth tooth counting from the front. With reference to the relative positions of the upper and lower teeth, determining which is and which is not "the canine" (ii.), no one, looking at the dentition of *Oreodon*, would be inclined to hesitate which teeth he shall call "canines"; yet the lower caniniform tooth shuts behind the upper, and, therefore, according to this test, it is not a true canine.

In the lemurs there are similarly four or six procumbent teeth occupying the front of the lower jaw, of which the outermost pair are called canines, although not in the smallest degree meriting that name for any other reason than that they close in front of the caniniform tooth of the upper jaw, for they are just like the incisors.

But it is in the *Insectivora*, which in some respects represent an ancient and generalised mammalian type, that the greatest difficulties occur.

To the mole no fewer than four dental formulæ have been assigned, all turning upon the identification of the canine. The difficulty is this: The upper tooth, which looks like a canine, has two roots, and it together with its deciduous predecessor (Spence Bate) is implanted within the limits of the premaxillary bone. With regard to this, Leche and Marsh point out that the canine is two-rooted in all the oldest known mammals, and that the reduction to one root goes hand in hand with the specialisation of its crown. Moreover, Leche does not attach much importance to its relation to the premaxillary bone, as he states that he is prepared to show that teeth rooted in the premaxilla in one species, and therefore incisors, are to be found in allied animals rooted in the maxilla. And besides this, the lower tooth, which answers the purpose of, and looks like, a canine, closes behind instead of, as in other insectivora, in front of the great upper teeth.

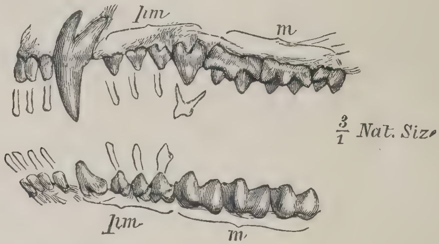

Fig. 193.—Upper and lower teeth of the common mole. In it, just as in *Oreodon*, the teeth which fulfil the functions of canines are not corresponding teeth in the upper and lower jaws.

Ericulus has a sharp, long, two-fanged tooth, in pattern of crown an enlarged premolar, in position of upper canine, and no caniniform tooth in lower jaw.

Centetes has typical canines, like a carnivore.

Hemicentetes. The so-called canine, differs in no respect from the premolars behind it.

Erinaceus. So-called upper canine, two-rooted, and like the premolars which follow behind it.

Gymnura. Upper canine-like tooth, has two roots; a single-rooted lower pointed tooth closes in front of it.

Macroscelis and *Petrodromus*. The third or outermost incisor, is two-rooted, long, and sharp, and plays the part of a canine.

Potamogale. A small tooth, in no respect different from the other premolars, is called a "canine."

Thus in some of the groups no tooth has been lengthened and pointed, so as to serve as a canine; in others it is the wrong tooth, *i.e.*, not the same tooth as in the Carnivora, or as in other Insectivora. Consequently in the Insectivora the elevation of a tooth into caniniform length and character is a mere adaptive modification, which may affect an incisor or a premolar, or no tooth at all. Wortman states that though a premolar is often so modified, no example is known of a lower incisor becoming caniniform to oppose an upper canine.

As regards the other premolars, there is no difficulty in their determination in those dentitions in which all four milk molars are present, and are succeeded by permanent successors, but this by no means always happens. In a very large majority of cases, the first tooth behind the canine is represented in one dentition only; hence it remains uncertain whether it is a milk tooth which persists, or a permanent tooth which has had no representative in the milk series.

M. F. Woodward ([10b]) discusses the question, pointing out that where there is no succession we may be dealing with a retarded member of an early or an accelerated member of a later set. In the mole, in which there is no succession as regards this tooth, the enamel-organ of pm1 does not appear till after those of the milk teeth, but contemporaneously with that of *pc*, which tooth, however, appears long before any of the other permanent teeth, so that the date of the appearance of its enamel-organ is not of much assistance. He further points out that in those cases amongst mammalia in which there is a succession of pm1 the canine is either vestigial, as in *Hyrax*, or is widely separated from the next premolar, as in *Tapirus indicus*, and further suggests that the usual suppression may be due to the great development of the canines. The first premolar is wanting or greatly reduced in all forms with great canines, and he thinks that the somewhat enlarged deciduous canine slightly stunts dpm1, while the enormous permanent canine crowds out and totally suppresses ppm1, so that he concludes by regarding the solitary pm1 as really a persistent milk tooth (as dpm1), a conclusion reached by Osborn on palæontological evidence.

The first premolar is apt to be very small, and it is remarkable that although it is usually almost functionless, it is apt to be long retained. Moreover, its eruption is apt to be later than that of the unquestionable second, third and fourth deciduous premolars, so that it has some claim to be considered as a member of the second series in those cases in which no tooth change occurs.

But these difficulties which have been briefly pointed out do not prevent us from forming a fairly definite idea of what the usual complete mammalian dentition is, and for brevity it is customary to write this out in symbols, thus :—

$$\mathrm{i}\,\frac{3}{3}\;\mathrm{c}\,\frac{1}{1}\;\mathrm{pm}\,\frac{4}{4}\;\mathrm{m}\,\frac{3}{3} = 44.$$

This is what is styled a typical mammalian dentition, and when teeth are absent from it, we can frequently say which are the absentees. But the occasional occurrence of a larger number of teeth amongst recent mammals, and the dentition observed amongst extinct mammals, have led Osborn (7) to consider that the typical dental formula of primitive mammals was

$$\frac{\mathrm{i}\,4,\ \mathrm{c}\,1,\ \mathrm{pm}\,4,\ \mathrm{m}\,8}{\mathrm{i}\,4,\ \mathrm{c}\,1,\ \mathrm{pm}\,4,\ \mathrm{m}\,8}.$$

As it is not always the same tooth which is absent, a fuller dental formula may be written thus :—

$$\frac{\mathrm{i}^1\,\mathrm{i}^2\,\mathrm{i}^3}{\mathrm{i}_1\,\mathrm{i}_2\,\mathrm{i}_3}\ \mathrm{c}\ \frac{1\ \mathrm{pm}^1\ \mathrm{pm}^2\ \mathrm{pm}^3\ \mathrm{pm}^4\ \mathrm{m}^1\ \mathrm{m}^2\ \mathrm{m}^3}{1\ \mathrm{pm}_1\ \mathrm{pm}_2\ \mathrm{pm}_3\ \mathrm{pm}_4\ \mathrm{m}_1\ \mathrm{m}_2\ \mathrm{m}_3},$$

$$\text{or } \mathrm{i}\,\frac{1\,.\,2\,.\,3}{1\,.\,2\,.\,3}\ \mathrm{c}\,\frac{1}{1}\ \mathrm{pm}\,\frac{1\,.\,2\,.\,3\,.\,4\,.}{1\,.\,2\,.\,3\,.\,4\,.}\ \mathrm{m}\,\frac{1\,.\,2\,.\,3}{1\,.\,2\,.\,3}.$$

The general, though not invariable, rule would appear to be that incisors were lost from the outer end, the third being absent when there are only two incisors, premolars from the front of the series being the first to drop out of the formula, and molars from the hinder end, the third being the first to disappear.

There are, however, many exceptions to this rule—*e.g.*, the first incisor is the first to disappear in the otter, walrus, and some few others, and a question has been raised as to the homologies of man's two incisors.

When premolars are missing, it is said that they are lost from the front of the series. Thus in the baboon the first and second premolars are absent, so that its dental formula written in full is :—

$$\mathrm{i}\,\frac{1\,.\,2\,.\,0}{1\,.\,2\,.\,0}\ \mathrm{c}\,\frac{1}{1}\ \mathrm{pm}\,\frac{0\,.\,0\,.\,3\,.\,4}{0\,.\,0\,.\,3\,.\,4}\ \mathrm{m}\,\frac{1\,.\,2\,.\,3}{1\,.\,2\,.\,3}.$$

This is generally true, but there are many exceptions, of which the following may be given.

In many bears the second premolar is often lost, as is also the third, but the first and the fourth are very constant ; this is also true of some bats.*

To make this more clear, Oldfield Thomas proposes to write out in full the dentition, thus :—

Bear :—

$$\mathrm{i}\,\frac{1\,.\,2\,.\,3}{1\,.\,2\,.\,3}\ \mathrm{c}\,\frac{1}{1}\ \mathrm{pm}\,\frac{1\,.\,0\,.\,0\,.\,4}{1\,.\,0\,.\,0\,.\,4}\ \mathrm{m}\,\frac{1\,.\,2\,.\,0}{1\,.\,2\,.\,3}.$$

Although modern marsupials have usually been considered to possess but three premolars, the original number was four, as in placental mammals. Thus in the extinct *Triconodon*,† which was probably marsupial, Thomas has shown that all four premolars are present, and it is the last or fourth which alone shows vertical succession.

From a study of the genus *Phascologale*, one of the *Dasyuridæ*, in which pm2 and pm3 are very constant, but pm4 variable and even reduced to a minute and functionless tooth in one species, it has been suggested that in *Dasyurus*, with its two premolars, it is pm4 that has disappeared.

---

* This is ascertained by the examination of allied forms, in which the third premolar is found to be so small that it might almost be termed vestigial.

† The systematic position of *Triconodon* is doubtful.

A comparison of many specimens (in one of which, *Phascologale*, four premolars were present, pm2 being smaller than the others, and a skull of *Dasyurus* in which a rudimentary tooth was present between its two premolars) indicates that the tooth which has disappeared was pm2.

$$\text{Thus Dasyurus has pms } \frac{1\,.\,0\,.\,3\,.\,0}{1\,.\,0\,.\,3\,.\,0},$$

$$\text{and Thylacinus pms } \frac{1\,.\,0\,.\,3\,.\,4}{1\,.\,0\,.\,3\,.\,4}.$$

[It is doubtful, however, whether the homologies of the teeth, when one or more of the series is absent, can be correctly interpreted from an examination of the skulls of adult animals, whether recent or fossil. In all cases where possible a microscopical investigation of the developing teeth should be made, in order to determine the position of any tooth vestiges if such happen to be present.

The homologies of the missing cheek-teeth in the marsupials will be further discussed in a subsequent chapter.]

Another difficulty arises from teeth which are beyond question of the permanent or replacing series, not persisting through the life of the animal, but being shed off.

The wart-hog is a conspicuous example of the early loss of teeth which clearly belong to the permanent series, all the teeth (premolar and molar) in front of the last great molar being cast off, and the dentition ultimately reduced to—

$$i\,\frac{2}{3}\;c\,\frac{1}{1}\;m\,\frac{1}{1}.$$

Amongst placental mammals the normal number of the molars is three.

The Tenrec, however, according to Oldfield Thomas, cuts a small fourth true molar late in life; this, coupled with its tritubercular pattern of molar teeth, is indicative of great antiquity. Of living mammals only the marsupials and *Otocyon*, a dog-like animal, have four true molars.

It is very unusual for the full typical number 44 to be exceeded; among recent placental mammals *Otocyon* exceeds it, but some fossil ungulates have more than the full number, and so have some marsupials.

Whether the immediate ancestral forms of mammalia were homodont like the Cetacea or the armadillo, or merely presented a much simpler and less differentiated series of teeth than recent mammals, may be a matter of doubt, but if we could place in series all the mammals that have ever existed it would be impossible to determine the point at which a differentiation towards some specialised type could properly be said to commence, so gradual are the transitions in all cases in which they are more or less fully known to us.

THE MILK DENTITION.

Many years ago Sir Richard Owen called attention to the fact that those mammals in which the teeth, situated in different parts of the mouth, are alike in form (homodont), as a rule, develop only one set of teeth. Those animals which, on the contrary, have teeth of different size and form in various parts of the mouth (heterodonts) develop two sets of teeth, a "milk" set, which is displaced by a permanent set.

But although this is true of a large number of animals if we take only functional teeth into account, even then exceptions are to be noted.

Thus the nine-banded armadillo (*Tatusia peba*) was considered to be truly homodont; its teeth are all very nearly alike, they are simple in form, and they grow from persistent pulps. Yet it has been shown by Rapp, Gervais, and Sir William Flower, to have a well-developed set of milk teeth, retained until the animal is of nearly full size.

Thus it is diphyodont, at the same time that it is a true homodont mammal. But no milk dentition has been definitely observed in the sloths, nor indeed at present has it been detected in other armadillos, with the exception of a doubtfully distinct species, so that as far as functional teeth are concerned many homodont animals are monophyodont.

But recent researches have clearly shown that the term monophyodont is no longer of much use, for even in apparently monophyodont animals the tooth-germs of another set of teeth, sometimes slightly calcified, sometimes yet further reduced, have been found. Hence there hardly remains room for doubt that the primitive condition of mammalia was that of diphyodontism or even of polyphyodontism, and that where only one set remains in full evidence the other has been lost by the suppression of that which is not needed.

Upon the whole, our information respecting the "milk" or deciduous dentition remains still defective; but much light has been thrown upon the subject by the recent investigations of Kükenthal, Röse, Leche, Oldfield Thomas, M. F. Woodward, Marett Tims, Wilson and Hill, and others.

The perpetual replacement of teeth lost or shed in regular course, which characterises the dentition of fish and reptiles (polyphyodont), finds no distinct parallel in the case of recent mammals, none of whom develop more than two functional sets of teeth, though Leche and many others believe that there are undoubted evidences of additional series.

[In this connection, attention may be drawn to an interesting example of polyphyodontism in a girl aged two years and nine months. Details of the case were communicated to the International Medical Congress held in London in 1913 by Dr. J. H. Gibbs, of Edinburgh.

In the right half of the mandible, which was considerably swollen, there were three definite rows of teeth, the uppermost of which were fully erupted. Separated by a thin shelf of bone occurred a second series consisting of a lateral incisor, a geminated canine, milk molars and a single permanent molar. The third row, again separated from the second by another thin plate of bone, contained also milk molars and a solitary permanent molar. The teeth of the third series, however, presented a remarkable feature: though situated in the right side of the mandible, morphologically they were left-sided teeth.

A crypt between the roots of the first erupted premolar indicated the existence of another dentition, though the developing tooth escaped observation.

Below the third series of teeth was a mass of soft connective tissue. From the fact that this mass contained columnar and cubical epithelium, Gibbs was of opinion that it afforded an indication of an attempt to develop a still further series. If this be the correct interpretation, five serial dentitions are represented.]

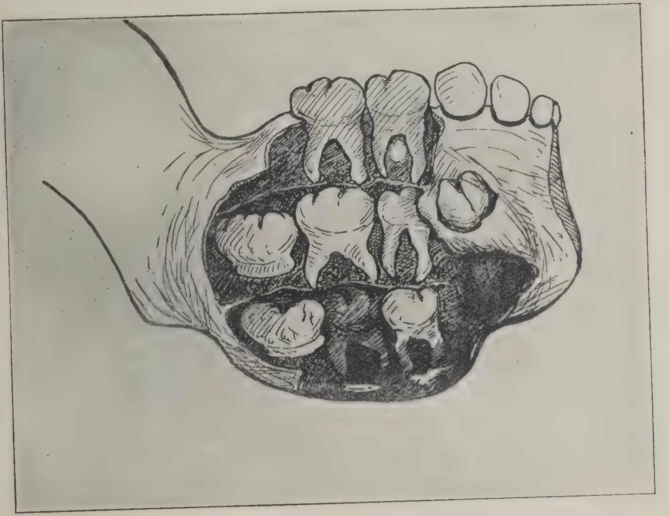

Fig. 194.—Drawing of the tumour made after the operation, showing the teeth in the relative positions. (Reproduced from Dr. J. H. Gibbs' article "Polyphyodontism in a Child" in the Transactions of the Seventeenth International Congress of Medicine, 1913, by permission of the author.)

The accompanying figure (Fig. 194) indicates the conditions present.

The deciduous or milk set of teeth may be of any degree of completeness. The milk teeth in man answer the requirements of the child up to the age of seven years, and in the Ungulata they commonly remain until the animal has assumed its adult proportions. On the other hand, in many "diphyodont" animals the milk teeth disappear very early indeed, as in the mole (see Fig. 193); whilst there are many instances of the milk teeth being absorbed *in utero*. So that, in the extent to which the milk teeth are developed, the greatest variability is found to exist.

A perfectly typical milk dentition represents with a considerable degree of accuracy, but upon a reduced scale, the adult dentition of the animal, any sexual differences which may exist in the latter being but very feebly marked in the former.

There are, however, several exceptions; such are found in the bats and in the edentates. Reference will be made to these subsequently.

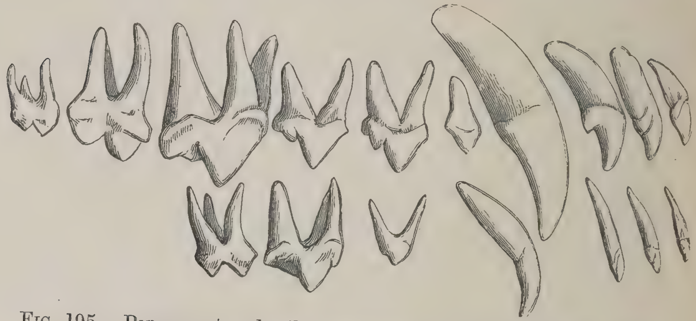

Fig. 195.—Permanent and milk dentitions of a dog; the latter is well developed. Natural size. (After Flower.)

As a general rule, the hindmost of the milk teeth bear more resemblance to the true molars which come up behind them than they do to the premolars which come up from below to displace them, the latter being generally of a somewhat simpler form.

In what may be termed the normal arrangement, each tooth of the milk series is vertically displaced by a tooth of the permanent series; but many examples may be cited of particular milk teeth which have no successors, and, on the contrary, of individual permanent teeth which have no deciduous predecessors.

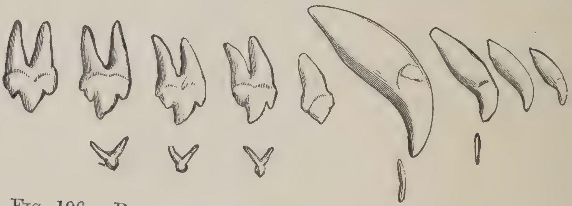

Fig. 196.—Permanent and milk dentitions of a seal (*Phoca greenlandica*). Natural size.

Although the views advocated by him have become in some respects obsolete, the papers of Sir William Flower (⁴) remain valuable in giving an instructive series of comparative development of milk dentitions, and from them the accompanying illustrations are borrowed:—

Within the order Carnivora, the dog and many others have a thoroughly well-developed set of milk teeth, which do service for some time ; in the bear the milk teeth are relatively smaller, and are shed very early ; in the seal they are vestigial and functionless, and are absorbed before birth, so that in the specimen figured the deciduous incisors had already disappeared.

In the elephant-seal the milk teeth are yet more feebly developed, and the difference between its dentition and that of the monophyodont homodont cetacean (*Grampus*) is not great, an observation which is the more interesting inasmuch as this seal in other characters than its teeth approaches towards the cetacean group. From these and other facts, Sir William Flower argued that the permanent set of teeth of diphyodont mammals correspond to the single set of monophyodont, and that the milk dentition, where it exists at all, would be something superadded.

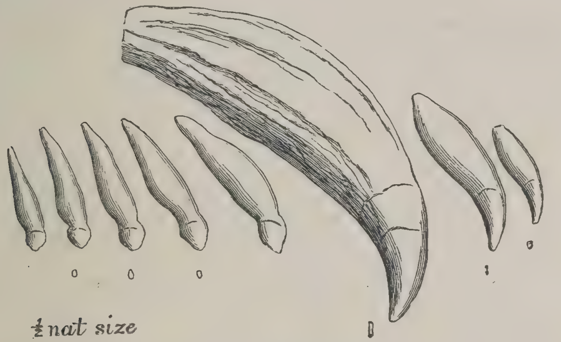

FIG. 197.—Permanent and milk dentitions of an elephant-seal (*Cystophora proboscidea*).

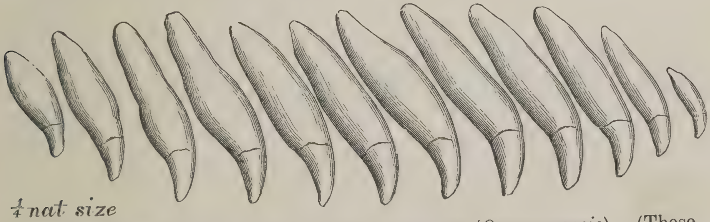

FIG. 198.—Teeth of the monophyodont grampus (*Orca capensis*). (These four figures are copied from Sir W. Flower's paper.)

This was a question upon which there was at that time room for doubt, and although the facts adduced by Sir William Flower afforded some grounds for argument that this was the true interpretation, yet the known facts of development pointed the other way.* Subsequent investigations carried out by means of complete series of serial sections of marsupial jaws by Leche and Kükenthal appeared to have rendered Flower's view untenable. In recent years further evidence has led to a resuscitation of that interpretation. As this evidence is mainly derived from a study of the tooth genesis in the marsupials, the question will be more fully discussed in a later chapter.

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* This discussion is now merely of historic interest. It was based on the view then current, that the monophyodout marsupials were on the direct line of descent

The question turns largely upon the interpretation attached to outgrowths of the tooth-band, which may or may not really represent aborted tooth-germs. The accompanying figure represents a stage of suppression of a milk tooth, in which, although the enamel-organ is but little differentiated, it is impossible to doubt that we have a true tooth-germ, as an irregular calcification has taken place at its end. (Cf. Fig. 199.) But in a great number of outgrowths of the tooth-band which have been regarded as representing tooth-germs there is no such calcification to settle the question.

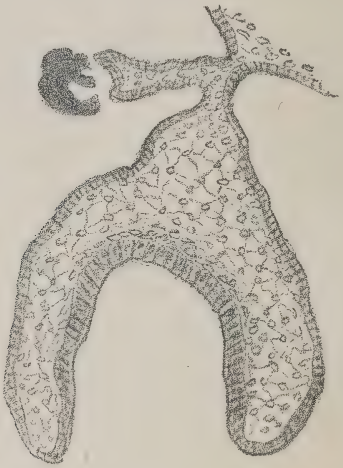

FIG. 199.—Permanent tooth-germ and aborted milk-germ of the canine of a hedgehog. × 100. (After M. F. Woodward.)

The epithelial lamina or tooth-band (Zahnleiste) descends into the mesoblastic tissue somewhat obliquely, inclining towards the tongue, and the buds which go on to form tooth-germs appear upon its labial side at, or close to, its end for the time being. Consequently, as its free end goes on growing deeper into the tissues on the lingual side of the already forming tooth-germ, we are justified in saying any additional specialisation of the dental lamina which is situated on the lingual side

of the Eutheria. In the marsupials but one tooth is replaced, pm4. Hence the conclusion that monophyodontism was primitive, the single pm4 representing a newly arising second dentition. The discussion centred around the question—Does the dentition of the marsupials represent the successional series of the Eutheria, with a deciduous set coming into being, or is it a persistent milk dentition, with one tooth only of the permanent series as yet evolved ?—H. W. M. T.

of a formed germ belongs to a later generation of teeth, and conversely that any similar growth of the lamina which lies on the labial side of a formed tooth-germ belongs to an antecedent generation.

Now, whilst in such a specimen as that figured on p. 258 we have in view at one time many generations of tooth-germs, we do not find in mammals that more than two attain to functional development, and the Fig. 200 III. represents what may be regarded as typical in the mammalia. Here we perceive that the germ of the successional tooth is at the end of the dental lamina—that it has, so to speak, used it all up, and that there is no prolongation beyond it. But this is by no means invariably the case. Sometimes we may find a little prolongation of the dental lamina beyond and to the lingual side of the developing successional germs, and this is regarded by many writers as an indication of a post-permanent dentition *in posse*. Similarly we may find an outgrowth to the labial side of the milk tooth-germ, and *à fortiori* of the successional germ, and this is nowadays sometimes interpreted as a vestigial premilk dentition.

But no one has, so far as is known, seen in any one specimen vestiges of all four at once *; had they done so, they would, of course, have to be interpreted as premilk (vestigial), milk (functional), permanent (functional) and post-permanent (vestigial). Röse believes that he has found evidences of a series antecedent to the premilk dentition in an early human fœtus, and a similar statement has recently been made in regard to the dugong (p. 496).

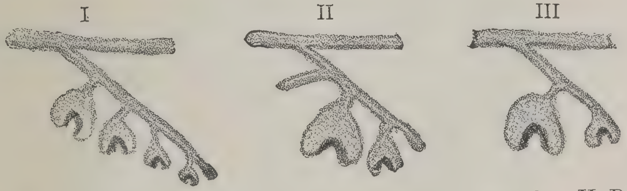

Fig. 200.—I. Diagram of indefinite succession in fish or reptiles. II. Diagram (hypothetical) of functional milk and permanent germs of mammalia, showing premilk and post-permanent rudiments. III. Diagram of typical mammalian succession, all tooth-germs save the milk and permanent having totally disappeared. In all the diagrams germs which proceed to functional calcification are marked by darker shading.

On the one hand, if mammals be descended from reptiles, which have for the most part an indefinite succession of teeth, it might perhaps be expected that some traces of the suppressed series of teeth might be found. On the other hand, it would indicate a retention of characters over a very long period of time, and tooth-germs may disappear *in toto*, as, for instance, the upper incisors of ruminants, although they have unquestionably been present at a comparatively recent period in the ancestors of existing ruminants.

As an example of the appearances, which lead to diversities of interpretation, the accompanying figure (Fig. 201) may be given. In it the milk tooth-germ is fully developed, and to its lingual side is the commencement of the germ of the successional tooth, both of these ultimately attaining to full functional development. But above the milk-germ and to its labial side is an outgrowth of the tooth-band, which, if it is to be regarded as an aborted tooth-germ at all, must be referable to a premilk series. It is, however, not accepted as certainly representing a tooth-germ by Marett Tims and others who have studied this specimen.

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* It is scarcely to be expected that all four dentitions should be found in any one specimen at the same time, for presuming them all to be present in the same animal, the development of the milk tooth will have sufficiently advanced to obliterate all traces of the premilk dentition before the post-permanent downgrowth will have become separated off from the enamel-organ of the successional tooth.—H. W. M. T.

Thus, it may be objected that many outgrowths of a tooth-band are not much differentiated, and that they are hardly worth calling tooth-germs, even with the added qualification "vestigial." But it must be remembered that mammals are of great antiquity, and that we should not expect to find any remains of long-lost structures highly differentiated.

[Bolk is of opinion that the labial outgrowths of the dental band

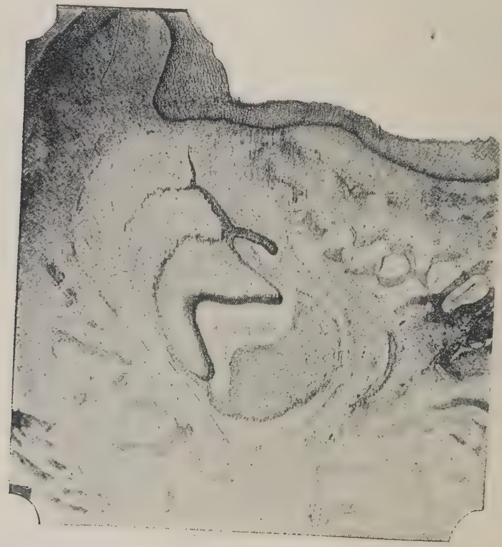

FIG. 201.—Tooth-germs of a pig, from a specimen given to the author by Dr. Marett Tims. The right is the lingual side of the specimen.

which have frequently been regarded as vestiges of a previous dental series are but traces of the dental glands which are well marked in reptiles. The labial outgrowth would, according to him, presumably represent a portion of the "accessory band" of reptiles, and consequently a relic of the reptilian "glandular band"; hence he does not admit the evidence of any premilk dentition in the mammalia.]

In view of the hypotheses which are occupying so much of the attention of naturalists upon the relations of the two (or more) sets of mammalian teeth, it becomes important to decide how much differentiation of the epithelial lamina we shall be justified in regarding as adequate evidence of a tooth-germ, but unfortunately there is no agreement on this fundamental point.

Kükenthal and Röse in particular, and following them a good many other writers, appear to be satisfied with remarkably little; almost any proliferation of the cells of the tooth-band leading to its being thickened or "swollen," so that it is bud-shaped on section, is for them a reduced tooth-germ; and Leche, whilst distinctly pointing out that neither a bud-shaped (as seen in section) enlargement of the band, nor even a connective tissue thickening about its free end, can be held to establish it as a tooth-germ, yet in practice seems to accept as tooth-germs a great many structures which show no more than this. It is true that such a swelling does take place where a tooth-germ is about to be formed. It is true, also, that in certain cases we are able to trace a downward series from a well-marked and calcified tooth-germ to ultimately nothing more than such a swelling; but it is also true that such swellings of the tooth-band do take place beyond the second tooth-germs of many mammals, and, in fact, in other positions where we have not the smallest ground for assuming that a tooth-germ has ever existed beyond the evidence of the swollen lamina itself.

Hence, as is clearly pointed out by Messrs. Wilson and Hill (9), mere enlargement of the tooth-band, even accompanied by some condensation of the mesoblastic tissue round it, is not adequate evidence. Of course, if it goes on to the bell-shaped cap with full differentiation of its outer and inner epithelia, and still more if there be the smallest calcification, no one can feel any scepticism. But unfortunately a very large proportion of the supposed germs upon which speculation is rife, and upon which theories are freely built, are merely of this doubtful character.

If we could find in any mammal all four sets of tooth-germs going on to calcification, or even to such an amount of differentiation as would show that the outgrowths were really aborting tooth-germs, all difficulty of interpretation would disappear; but unfortunately this is not the case. We do not find all four at once; neither are the supposed rudiments so far differentiated as to put their nature beyond all doubt (cf. p. 319).

So when we have to deal with what are apparently three sets of rudiments successional to one another, the question always has to be decided for the particular case, To which of the supposed five dentitions do the functional teeth of the individual belong? before we can assign a place to the extra rudiment, if, indeed, true tooth rudiment it be.

In the whole group of marsupials (with the exception of the wombat) no tooth change had been demonstrated except in the case of an individual tooth, the last premolar, but here the vertical succession is curiously constant, though in the case of some of the *Dasyuridæ* it is shown in process of reduction and disappearance. The question as to whether this is a true case of tooth succession will be fully discussed in the chapter dealing with the dentition of marsupials.

This succession of a single tooth had become established in very early geological times (*e.g.*, *Triconodon*), and has been retained with remarkable constancy. Then came the researches of Kükenthal and Röse, who showed that the tooth-band, beyond and to the lingual side of the germs of the functional marsupial teeth, becomes swollen, and they gave to these enlargements the full significance of tooth-germs (which has since been denied them by Wilson and Hill). Kükenthal regarded the functional dentition of marsupials as being a persistent milk dentition, with remaining rudiments of a suppressed (or first appearing?) second dentition, a view which obtained a large amount of acceptance.

Leche subsequently discovered that actual calcification, though of an abortive kind, does take place in *Myrmecobius* in germs which obviously belong to an earlier series than the functional teeth. On the basis of Kükenthal's discovery, this writer strongly held to the view that the functional teeth of all marsupials are persistent milk teeth; he was hence compelled to interpret these rudiments as belonging to a "premilk" series, for they lay to the labial side of the functional germ. This interpretation rests entirely upon the correctness of the identification of the functional teeth of the whole marsupial group as persistent milk teeth. And this interpretation of the functional teeth of marsupials in turn rests upon the fact that supposed germs of a successional set—that is to say, germs upon the lingual side—of the developing functional teeth have been recognised in a considerable number of marsupials by Kükenthal, Leche, Woodward, Röse, Tims, and others, so that, if we acknowledge these as tooth-germs at all, the functional teeth are certainly not the latest set represented by vestiges, which would seem to be in favour of the view that the teeth of the marsupials really are persistent milk teeth.

However, even granting this, there remains a shadow of doubt, for Marett Tims thinks that, inasmuch as in *Didelphys* Röse has seen what he regards as three sets of germs, and it was the middle one which developed, it is possible that after all the milk teeth are suppressed, the permanent teeth developed, and a post-permanent set of vestigial germs * are still to be found. The matter is still open to argument.

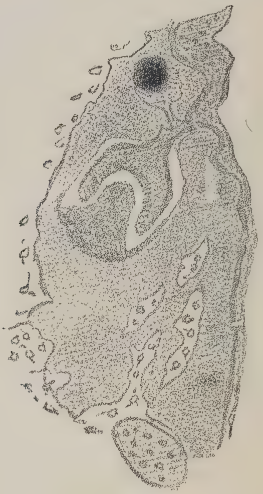

FIG. 202.—*Myrmecobius*. × 50. Tooth-germ of functional canine, to the left of which is seen a slightly calcified rudiment of a tooth of an earlier generation. (After Leche, according to whose interpretation they represent germs of a milk canine and of a premilk canine.)

But if the one set of functional teeth of marsupials are permanent teeth, then Leche's premilk teeth become ordinary aborted milk teeth, and *Myrmecobius* merely stands alone among marsupials in having some calcification occurring in both sets.†

Woodward thus puts the state of ideas upon the subject of the premilk dentitions: "In the anterior part of the jaw of the marsupials we find the following sets of teeth: (1) a small vestigial set, often calcified ; (2) a large functional set ; and (3) a series of lingually placed swellings of the dental lamina (Kükenthal, Röse, Leche, and Woodward) closely resembling in appearance the first indication of the successional germs in the Placentalia. It is generally believed that the second set represents the milk dentition, and the third the reappearing permanent teeth of higher mammals, the first vestigial set being regarded as premilk dentition. If the structures described by Röse and Leche in man, the ox and the hedgehog, are the homologues of the calcified labial set of the marsupials, then there can be no doubt that this latter is a premilk dentition ; but these structures in the Placentalia are slight, though said to be constant, and some may doubt the correctness of this interpretation, especially on comparing these labial teeth with the undoubted reduced milk dentition in many insectivores, and they may consequently be inclined to regard, as Tims has, the labial toothlets of the marsupials as reduced milk teeth, and thus revert to the discarded Flower and Thomas hypothesis. It will no doubt be difficult to convince such believers that their interpretation is incorrect until we can find some premilk teeth in the Placentalia better developed than those of Leche and Röse, and we can only admit that ontogeny is not yet as conclusive on the point as one could wish." *

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* This opinion rests not merely upon the conditions found in the marsupials, but also on a comparison with the conditions existing in many Eutheria.—H. W. M. T.

† Uncalcified representatives of the so-called "premilk" dentition are to be found in other marsupials.—H. W. M. T.

And, finally, Messrs. Wilson and Hill (*loc. cit.*),† finding in *Perameles* some vestiges (calcified) corresponding to those of Leche in *Myrmecobius*, and wholly denying the right of the Kükenthal and Röse "swellings" to the lingual side of the functional germs to be regarded as tooth-germs at all, reopen the whole question, and would say of the marsupials that they all present a more or less completely aborted milk dentition, and a functional permanent dentition homologous with that of placental mammals, and thus confirm the view previously suggested by Marett Tims.

Though personally the author is inclined to accept the views of Messrs. Wilson and Hill, and of Marett Tims, they have not as yet found universal credence. Thus Carlsson holds that the functional dentition is lacteal, and that rudiments of permanent teeth do exist, of which only pm3 is fully developed. Adloff, Bild, and Deppendorf also accept Leche's prelacteals.

Bild affirms that traces of prelacteal germs are found in pigs, but his figures are not very conclusive as to whether the outgrowths in this situation really deserve to be considered as tooth-germs, and Adloff says that prelacteal rudiments exist in rodents also, but these too may be regarded as doubtful.

As the reader will have gathered, the question of the existence of traces of either prelacteal or post-permanent dentition is by no means yet settled. To roughly summarise recent views, it may be said that, according to Leche's latest dicta, in marsupials the functional teeth belong to the milk dentition. There are rudiments, sometimes calcified, of a premilk set ; of the "permanent" teeth one only is fully calcified, and often functional, the others are vestiges.

In placental mammals there are but small traces, probably never calcified, of a premilk series. The milk teeth (with the possible exception of the true molars ; see *infra*) never persist through the whole life of the animal, but a " permanent " set replaces them in the adult animal. A " post-permanent " set is represented in some animals by bands beyond the permanent tooth-germs, but these never calcify.

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* This quotation is taken from a paper by M. F. Woodward published in the *Anatomischer Anzeiger* in 1896. Since that date evidence has been gradually accumulating in favour of the view that the functional dentition of the marsupials does correspond to the Eutherian successional series.—H. W. M. T.

† This paper, though published in the same year as that by Woodward, did not appear until some months later.—H. W. M. T.

The milk dentitions occur in various degrees of reduction, thus :

a. One (for instance, dpm¹ in most mammals) or more (*e.g.*, *Erinaceidæ*) fail to attain to full calcification, without the rest of the milk teeth being aborted.

b. The whole milk dentition (except as above, and the true molars *) is more or less rudimentary (*e.g.*, *Pinnipedia*) ; and in some forms is absorbed without even being cut, as in some *Phocidæ*, *Rodentia*, and *Chiroptera*.

c. The milk dentition (except as regards the true molars as referable to it) does not attain to any calcification at all (shrews and many rodents).

d. The milk dentition is neither represented by rudimentary nor by erupting teeth (? *Bradypus*).

This is a considerable modification of Leche's earlier views, but it does not meet with universal acceptance. Thus Kükenthal (and Leche formerly) holds that the teeth of Cetacea are milk teeth, and that it is the permanent series in them which is suppressed, though Leche regards it as still somewhat an open question.

As regards the true molars, several ideas have been propounded :—

1. That, as suggested by Owen and others, these teeth, having had no predecessors, and having arisen from the primitive tooth-band, must be regarded as members of the milk series (Kükenthal, Röse, Leche, &c.).

2. That they belong to the second or permanent series of dentitions (Woodward, Magitot, Marett Tims, &c.).

3. That they are not homologous with either, but represent the two series by a fusion of germs or by using up the material whence two series might have been founded (Kükenthal's later view, Schwalbe).

4. That each true molar is the terminal member of a separate series of successive dentitions, the rest being all lost.

With regard to 3, Marett Tims (⁸), whilst discussing the genesis of tooth forms, expresses a belief that each molar may represent an antero-posterior fusion of two teeth belonging to the same series, but he rejects Kükenthal's theory that a lateral fusion of two teeth belonging to successive series has taken place. Adloff, however, states that he has seen the fusion of a prelacteal germ in rodents with a lacteal tooth ; Bild affirms the same thing in pigs, and Kükenthal in the dugong, all therefore supporting the concrescence theory. Hopewell-Smith and Marett Tims have also recently described appearances in the developing molars of *Macropus billardieri* which may indicate a fusion of enamel-organs (Fig. 203). A fusion of cusps is known to occur in *Ceratodus* and in *Sphenodon* among lower vertebrates.

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* This exception is made on the assumption that the molar teeth belong to the milk series, which is doubtful.—H. W. M. T.

The question is therefore still *sub judice*. Lydekker has, however, been influenced by the evidence accumulated to the extent of disclaiming the views which, in common with Flower, he formerly held (4), and now regards the dentition of marsupials, disregarding for the moment the replacing tooth, as consisting of persistent milk teeth plus true molars. This leads him to further inferences, which are of considerable importance. Thus, he regards the original mammalian dentition as consisting of milk teeth plus true molars. These last he considers as homologous with the milk dentition rather than with the so-called permanent dentition, replacing teeth (or teeth of the second dentition), which may or may not occur, and which he regards as the thing superadded and not as being the constant typical set of teeth. In this connection he points out that the hindmost milk molar always closely resembles the first true molar, so that there is no abrupt transition at this point where both are in place at the same time. He does not agree with Ameghino (p. 307) that it is desirable to abandon the term premolar, but, on the contrary, would prefer to designate the milk molars (as ordinarily understood) as milk premolars, teeth which may or may not be displaced by permanent premolars. Hence he would write down the milk dentition of man as

$$\mathrm{di}\,\frac{2}{2}\;\mathrm{dc}\,\frac{1}{1}\;\mathrm{dpm}\,\frac{2}{2},$$

and the permanent dentition as

$$\mathrm{i}\,\frac{2}{2}\;\mathrm{c}\,\frac{1}{1}\;\mathrm{pm}\,\frac{2}{2}\;\mathrm{m}\,\frac{3}{3}.$$

For many years past it has been usual to consider that there was a marked difference in the dental formulæ of marsupials and of placental mammals, it being held that the former had but three premolars and four true molars, whilst the latter had four premolars and three true molars. Oldfield Thomas has shown that this is not certain, and the advance of palæontology has thrown additional difficulties in the way of accepting the distinction, so that Lydekker and many others now hold that the typical dental formula is the same for both, namely, four premolars and three true molars; but to this subject it will be necessary to recur in dealing with the teeth of marsupials.

There is a reason, or some show of a reason, for the succession taking place as far back as the premolars, the molars being exempt from change. In all mammals the whole length of the jaw, at the time of birth and afterwards, is occupied by tooth-germs and afterwards by teeth. It is well ascertained that the manner of growth in the jaw is by backward elongation, and that that portion which is occupied by the molars actually does not exist at the time of birth, so that the tooth-band, boring backwards in this region, dips down and has to lose its vertical connection with the epithelium of the surface. Tooth-change might therefore be expected to be limited, as in fact it is, to that portion of the jaws which exists early, while the animal is small. A succession of teeth could not exist in the molar region, because during the reign of the milk teeth in front the molar region itself does not exist.

[There is reason for believing that predecessors to the true molars once existed in several animals, *e.g.*, guinea-pig, as "concentric epithelial bodies" occur to the labial side of the developing molars. These bodies are precisely similar to those figured and described by Wilson and Hill in *Ornithorhynchus*, and shown by them to be tooth vestiges.]

If we consider that the point of the primitive diphyodontism of the mammals is established, and that they are probably descended from polyphyodont ancestors, no further explanation of the existence of successional teeth is called for. But the view propounded by Baume and adopted by Oscar Schmidt should just be noticed. They suggest that the two dentitions were originally disposed in line, and that the origin of successional teeth can be traced back to the shortening of the facial region, which gave no room for the full number of tooth-germs to lie side by side, the result of this crowding being that they came to lie upon the top of one another, each alternate one becoming displaced and retarded; then that the teeth lying nearest to the surface, having to be used first, get developed first, and thus the milk teeth are placed at a disadvantage owing to the hostile position of their successors, which cause their absorption and ejection.

The investigation of these questions is further complicated by the fact that there are quite numerous instances of "permanent" teeth, that is teeth unquestionably belonging to the second set, which are shed off early, and do not remain in place through the lifetime of the animal. An example of this is to be found in the wart-hog (*Phacochœrus*), which loses successively all its premolars and the first and second true molars, the last true molar alone being truly persistent.

It has already been mentioned that amongst homodonts no succession of teeth has been observed in the Cetacea; but Kükenthal states that the teeth of toothed whales (*Beluga*, *Tarsiops*, and *Globiocephus*) are the milk teeth, inasmuch as germs of successional teeth which never cut the gum are to be found to their inner sides, while Leche considers the evidence insufficient.*

In the shrews the milk series is very greatly reduced (p. 390), while in the bats the milk teeth are homodont and their successors heterodont. In those edentates in which a succession is known, the first teeth are heterodont, their successors homodont. No succession is known to take place in any of the Edentata, save the armadillo, *Dasypus novemcinctus* (Martin), and in the very aberrant form *Orycteropus* (see p. 426). Amongst heterodonts there are several rodents which have no deciduous teeth, *e.g.*, the rat. Probably the dugong has deciduous incisors, but no other milk teeth. The elephant has no vertical succession, save in the incisors, but instead has a succession of teeth from behind forwards in the molar region.

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* The arguments as to the interpretation of the cetacean dentition are similar to those given above in relation to the marsupial dentition and to the homologies of the molar teeth.—H. W. M. T.

As regards the " premilk " and post-permanent germs, it may be repeated that both alike stand or fall according to the import attached to the prolongations of the dental lamina beyond the permanent tooth-germs. If these swellings are not tooth-germs, then there is nothing to lead us to speak of a post-permanent dentition, as no one has seen a well-differentiated tooth-germ, much less any calcification in this region. Again, if they be not tooth-germs, then the functional teeth of marsupials are ordinary permanent teeth, and the " premilk " germs of Leche, Woodward and others, described also, but not so styled, by Marett Tims and Wilson and Hill, which do go on sometimes to abortive calcifications, are merely the ordinary milk set in a certain stage of suppression. The author regards both " premilk " and " post-permanent " rudiments as at present hypothetical, and the evidence insufficient to establish their existence.* But the literature upon this subject has become so profuse, and the data require such detailed descriptions, that it is quite impossible to enter into the discussion in the pages of a small text-book, so the reader must be referred to the original sources, of which he will find an excellent summary in Messrs. Wilson and Hill's paper (9).

[The foregoing account of the tooth succession of the mammalian dentitions gives a *résumé* of the main current views. Reference must now be made to the theories recently advanced by Bolk, and which are at variance with the views hitherto held.

As stated in a previous chapter, Bolk considers the mammalian enamel-organ to be a double structure and that the fully formed tooth represents a fusion of two tooth generations (*vide* chapter Dimer theory).

The process of tooth replacement in reptiles Bolk regards as a totally different phenomenon from that which occurs in the mammals ; hence the diphyodontism of the latter is not to be derived from the polyphyodontism of the former. The typical difference is that the functioning teeth of the reptiles comprise members of two series (*i.e.*, exostichos and endostichos), *i.e.*, " *hamastichical*," and as the members of the two series alternate regularly throughout the jaw, Bolk defines the dentition as “*isocrasic hamastichical,*” whereas in mammals the two rows function one after another, *i.e.*, “*choristichical.*” The marsupials, according to this writer, occupy an intermediate position, in that he considers some of the teeth belong to the milk series and others to the successional, *i.e.*, hamastichical, but their relative positions are not regularly

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* There is now less reason for hesitation in accepting the evidence of the presence of premilk vestiges than was formerly the case. Doubt may still exist as to the value of the post-permanent downgrowths of the dental lamina.—H. W. M. T.

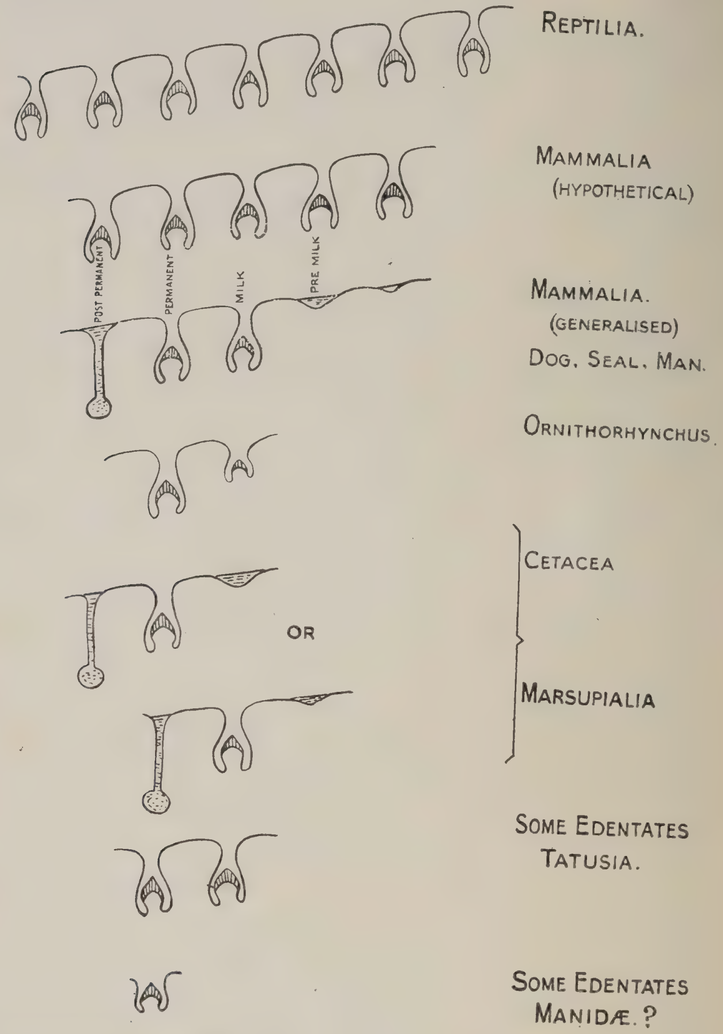
REPTILIA.
MAMMALIA
(HYPOTHETICAL)
POST PERMANENT
PERMANENT
MILK
PRE MILK
MAMMALIA.
(GENERALISED)
DOG. SEAL. MAN.
ORNITHORHYNCHUS.
CETACEA
OR
MARSUPIALIA
SOME EDENTATES
TATUSIA.
SOME EDENTATES
MANIDÆ.?

DIAGRAM SHOWING THE NUMBER OF DENTITIONS REPRESENTED IN THE VARIOUS GROUPS OF THE MAMMALIA. (*MARETT TIMS*) alternate, and therefore not numerically equal; hence the dentition is "*anisocrasic hamastichical.*"

To quote Bolk's own words (p. 723), "the simplest conception is that with reptiles the dental matrix extends its productivity over the whole life of the individual, giving birth each time to an elementary tooth, while on the other hand, with mammals the whole productivity of a dental matrix is exhausted in the formation of a single product, containing potentially a larger number of elementary teeth, a number of dental generations. A whole dental family of the reptiles has, as it were, been condensed in a mammalian tooth" (3).

Bolk's views are so revolutionary that his original communications should be consulted as to the details upon which they are based. These have been attacked strongly by Adloff (1), mainly on theoretical grounds.]

In the accompanying diagram an attempt has been made to summarise at a glance the present position of our knowledge with regard to the interpretation of the mammalian dentitions.

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CHAPTER XIII.

EVOLUTION OF THE FORMS OF TEETH.

Our knowledge of extinct mammalian forms being very largely based upon their teeth, which are often better preserved than other parts owing to the extreme hardness of their tissues, much attention has been devoted to the manner in which their patterns have been arrived at and to the forces which may be supposed to have acted in their modification.

It has been suggested by J. A. Ryder (8) that the pattern of the molar teeth of Herbivora is the result of the extent and direction of the excursions of the mandible when it is in use, and so depends upon the form of the glenoid cavity and of the condyle ; that hence the greatest modification is to be found nearest to the articulation where the greatest force is exerted. Thus " bunodont " animals, *i.e.*, those that have rounded conical cusps upon their short-rooted teeth, have a cylindrical condyle ; selenodonts, or those with crescentic ridges on the crown surfaces of the molars, have a condyle which is expanded and plane ; while lophodonts, or those with transversely ridged teeth, have a globular condyle.

It has been pointed out by Cope that in many instances the articular surfaces of bones assume forms very similar to those which would be modelled by two somewhat plastic masses working upon one another, and it is a familiar fact that if a dislocation be left unreduced, the surfaces of bone in contact will become so altered as to form a sort of articulation in the new place.

But even if we grant the one much-disputed point, namely, that characters acquired by the individual in its own lifetime can be transmitted to its offspring, there is a special difficulty remaining in the case of teeth in adopting the simple mechanical explanation that the teeth are, so to speak, drawn or squeezed into their forms, whether in one or in ten thousand generations. For, unlike a bone, which is very much alive, and is constantly growing and being renewed after it has come into use, that portion of the tooth which is subject to these direct influences is hard and rigid, and its form, whatever it be, in that individual is unalterable. In order to alter the form of a masticating surface by direct mechanical means, the influence would seem to need to be brought to bear upon the teeth while they are yet soft, when they are still buried within the jaw in their bony crypts. And we cannot safely assume that structures like enamel-covered dentine can be altered by pressure, the essential character of dentine being its elasticity, and that of enamel its rigidity.

It therefore follows that the tooth is of a nature very little likely either to be deformed by pressure, or being deformed, to retain the deformity.

Cope, quoting this objection, states that Kölliker and others have established the existence of osteoblasts on dentine as well as upon bone, but this in no way appears to the author to meet the objection, as the only place where osteoblasts can occur is on the inside of the dentine, *i.e.*, on the walls of the pulp cavity, and it is not therefore easily understood how they can help the matter short of removing the whole thickness of the dentine. Moreover, it would appear that we have no right to assume that the lateral excursions of the jaw and the form of the condyle antedated the special form of the teeth.

Thus, however tempting the doctrine of Cope's kinetogenesis, by which the very accurate articulation of the cusps of the teeth with one another, as well as their variety of forms, is sought to be accounted for, it hardly commends itself as possible, at all events in the form in which it was promulgated.

It has been pointed out by Osborn that in the palæontological record it is found that the points of greatest wear in the molars of more ancient forms are just the places in which in succeeding periods of time new cusps appear.

Granting the inheritance of acquired characters, this seems more easy to follow. It is a familiar fact that the stimulus of excessive wear, conveyed probably through the dentinal fibre, does stimulate the corresponding odontoblasts to increased action, and that new dentine is built on to the wall of the pulp cavity to thicken it at the threatened point.

To the mind of the Neo-Lamarckian it would not be a long step from this to the earlier and stronger development of dentine at this point in a succeeding generation, *i.e.*, to the development of a new cusp. But if we accept this idea, then we are confronted with a difficulty in that Cope's view of the plastic yielding, if it may be so expressed, and Osborn's idea of a reaction leading to an increased resistance, seem contradictory, as they would both arise as a consequence of forces not very different acting upon a tooth.

Moreover, Cope's idea seems to involve a greater degree of fixity in the attachment of the teeth than practical experience finds to obtain. For a tooth quickly yields to a constant or frequently recurrent pressure, especially in any lateral direction, so that one would expect the teeth of the ruminant to move in their sockets rather than to be affected in form. Cope himself recognises this as a factor which has determined the outward leaning of the incisor teeth of the lemurs, which perhaps use their front teeth to comb out their fur.

Another difficulty arises from the fact that in the mutual adaptation of the working surfaces the development of a cusp on the one tooth involves a depression on the other, yet action and reaction must have been equal on the two points.

Wortman extends the idea of kinetogenesis yet further, thinking that the cingulum may be a wrinkle or fold produced by long-continued pressure applied vertically, and that division of single roots into two may have resulted from a backward and forward rocking of the tooth in mastication.

Cope thus formulated the influences which he conceived to be the most important :—

1. Increase of size of a tooth, or of a part of a tooth, is due to increased use within a certain maximum of capacity for increased nutrition.

2. The change of direction and use of a tooth takes place away from the direction of greatest, and in the direction of least, resistance.

3. It follows from their greater flexibility that the crests or crowns of teeth yield to strains more readily than do the cusps.

4. The increase in the length of crests and cusps in all directions, and therefore the plications of the same, is directly as the irritation from use to which their apices and edges are subjected up to the limit set by the destructive effects of such use, or by the recuperative energy of nutrition.

5. The direction of growth of the branches of a V, or of the horns of a crescent, will be in the direction of movement of the corresponding parts of the opposite jaw.

Apart from the investigation of the actual forces at work, naturalists have sought to discover the probable ancestral form of mammalian teeth, and the steps by which they have arrived at their ultimate complexity.

The earliest theory is that known as concrescence, under which it is suggested by Kükenthal and Röse (though the idea is much older than their time*) that the occurrence of multicuspid teeth may be explained by the shortening of the jaw and consequent crowding of the teeth leading to the coalescence of several simple conical teeth to form a single tooth with several cusps ; thus they would regard the five-cusped human molars as derived from the coalescence into one tooth of five originally distinct simple conical teeth. This view was supported by Virchow, who thought that a case in which the place of a molar had been taken by three peg-shaped denticles with separate roots was an instance of atavism. This coalescence might take place in the length of the jaw, and result in a shortened jaw with a smaller number of more complex teeth, or it might take place laterally, in which case the teeth fused would be of successive series, *i.e.*, of different dentitions. On this latter supposition Kükenthal would regard a molar tooth with its outer and inner cusps as the product of the lateral fusion of a milk tooth or two milk teeth with one or two of the permanent series.†

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* As far as I have been able to discover, Gervais (1854) was the first writer to advance any theory in explanation of the evolution of the molar pattern. His theory was practically that now known as the concrescence theory.—H. W. M. T.

† The most recent discussion of the concrescence theory is that by Bolk (2), who advances certain modifications of his own, for a detailed account of which the reader is referred to his somewhat lengthy paper.—H. W. M. T.

Although it is true that some observers have believed that they have seen evidence of the coalescence of more or less rudimentary tooth-germs with the germs of functionally developed teeth in their immediate neighbourhood, there is but little evidence that such fusion, even if it does take place at all, has the effect of adding cusps, or otherwise altering the form of the absorbing germ. Hopewell-Smith and Marett Tims have figured in a recent paper what they suggest as possible evidence of the fusion of tooth-germs in the molar teeth of a wallaby (3). In the case of *Ceratodus* (p. 265), and of *Sphenodon* (p. 284), the coalescence of tooth-germs, originally distinct, to make up a continuous sheathing mass of dental tissue has been observed. Marett Tims, whilst rejecting Kükenthal's idea that molars represent the fusion of teeth belonging to two successive series, has expressed the opinion that it is possible that they may be built up by the fusion of two teeth antero-posteriorly, of two teeth of the same series in fact (10). Ameghino has pointed out that the numbers of individual teeth and of cusps upon each tooth stand in an inverse ratio to one another (1).

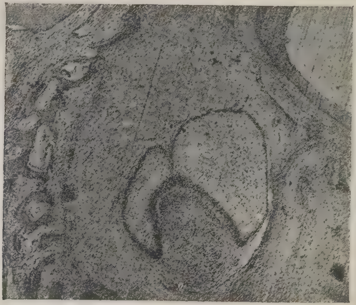

Fig. 203.—Showing the subdivision of the enamel-organ into two parts. ? a fusion of two distinct enamel-organs. (Hopewell-Smith and Tims, Proc. Zool. Soc. Lond., 1911.)

Still palæontology does not afford much definite support to the concrescence theory. Of course the geological record is very imperfect, and there are but few cases in which we can watch the gradual evolution of a complex tooth form over a long series of ages, but where we can, concrescence does not appear to afford a good explanation of the facts observed. Another difficulty in accepting the concrescence theory is pointed out by Osborn. Long after a settled form has been arrived at and perpetuated for long periods of time, long after, so to speak, the component separate teeth have been forgotten, we have the phenomenon of new cusps arising. It is difficult to suppose in such a case that a long-lost tooth thus reappears to make a new cusp, and hence there must be some other way of genesis for added cusps.

The cingulum theory is another explanation which has been offered, and is strongly urged by Marett Tims (*loc. cit.*). The cingulum is a ridge which surrounds the neck of a tooth, and is a very ancient structure, for all primitive teeth are completely surrounded by it, and even the strongest advocates of the tritubercular theory, to which reference will subsequently be made, recognise its importance. Thus Osborn says, "As is well known, the hypocone is an upgrowth from the cingulum. By its disappearance in some regions, and by its elevation into prominence in others, the form of a tooth may become profoundly modified, and it thus comes to be regarded as a sort of mother of cusps." Marett Tims leans to the cingulum hypothesis as explaining much of the evolution of tooth forms in complexity, and mention may be made of a very instructive series of comparisons of the molar teeth of Insectivora by Mivart (5), pointing out that within the limits of this group a great variety of patterns is met with, the several modifications being connected by transitional forms. A V-shaped tooth of tritubercular aspect occurs in some of the Insectivora of Madagascar and Africa, and in many others there is a more complex or W-shaped pattern.

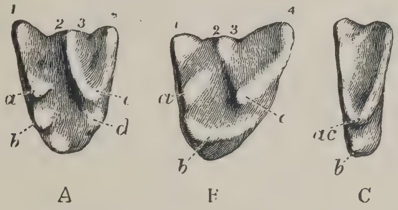

FIG. 204.—Upper molar teeth of (A) *Urotrichus*; (B) mole (*Talpa*); (C) *Chrysochloris* (the Cape iridescent mole). The four principal cusps (Mivart) are lettered *a*, *b*, *c*, *d*, the others being elevations of the cingulum of secondary importance. Woodward suggests that their homologies are: *a*. Paracone. *b*. Protocone. *c*. Metacone. *d*. Hypocone.

Often upon the upper molar teeth of Insectivora there are four principal cusps (lettered *a*, *b*, *c*, *d*, in the figure) which are more or less connected by ridges; such simple teeth are met with in the elephant mouse (*Macroscelides*) and hedgehog. The cingulum is well developed in most of the group, and the further complexity of the crowns, which often bristle with sharp points, is brought about by the elevation of the cingulum into long sharp points, equalling or exceeding in length the principal cusps of the tooth.

Thus in *Urotrichus*, a Japanese creature having affinities with the mole, the external cingulum is elevated into three distinct pointed cusps, united by ridges with the two principal cusps, an arrangement which gives a sort of W pattern to the surface, while to the inner side the cingulum forms another cusp, so that there are in all eight cusps; the common mole has the third cusp developed from the outer cingulum, but its two inner principal cusps are fused together and lose their distinctiveness. The suppression and fusion of cusps is carried to a much greater extent in the compressed teeth of the iridescent mole (*Chrysochloris*), but there are intermediate forms which render it easy to identify its reduced parts with those corresponding to them in the mole or in *Urotrichus*.

Speaking generally, it may be said that new cusps are added to the number already existing by the cingulum becoming elevated into points ; it is not very unusual to see subsidiary cusps obviously originating in this way upon human molars.

Ridges may variously connect the cusps. Mivart suggests that the coalescence of two or more cusps to form an exceedingly elevated point is illustrated by the carnassial tooth of Carnivora. To this transformation certain marsupial teeth form the clue, as they afford unquestionable evidence of such coalescence by a gradational series of small modifications in this direction occurring in allied creatures. But this view is at variance with that of Cope and Osborn. Whilst Mivart regarded the simple tritubercular tooth as derived by compression and fusion of cusps from the others, they would advocate a course of modification the converse of this.

The tritubercular theory, which has a large literature of its own, owes its present form chiefly to the writings of Cope, Osborn, and others of the American school of naturalists. On the Continent it has some adherents, but in this country it has for the most part received only a guarded and partial recognition. Its essential feature is that in the evolution of teeth from the simple cone a stage was reached at an early period in which three cusps were arranged in a triangle. Not only was this tritubercular tooth reached early, but it was possessed by a considerable number of the earlier mammals, and is still retained in some existing forms. This triangle of cusps, or trigon, once attained, is believed to have shown such fixity of type that not only has it come down comparatively unchanged in some animals to the present day, but that it can be traced, and its component cusps identified, even in teeth which have become more complex in form and have lost all superficial resemblance to the primitive tritubercular tooth.

The early steps may be thus described : To the primitive cone (protocone) were added two lesser cones, one in front (paracone) and one behind (metacone). To such a tooth with its three cusps in an antero-posterior linear series the name triconodont is applied, and is to be seen in the teeth of the fossil *Triconodon*. The accessory anterior and posterior cusps enlarged and became displaced sideways, so that there came to be on the upper teeth two outer and one inner cusp, and on the lower two inner and one outer cusp.

[Such a tooth has now assumed the tritubercular pattern, *i.e.*, having a triangular crown surface with a cusp at each angle. In the upper molars the internal apical cusp is the protocone, and is regarded as the representative of the primitive haplodont cone.

The anterior basal cone is the paracone, the posterior the metacone. In order to distinguish the corresponding cusps in the lower molars, the suffix - *id* is added. Hence they are named protoconid, paraconid, and metaconid respectively. The triangular pattern of the upper molars is reversed in the lower teeth, so that the apical protoconid is placed externally, the paraconid and metaconid being at the anterior and posterior angles respectively, and placed to the inner side of the crown surface.]

Fig. 205.

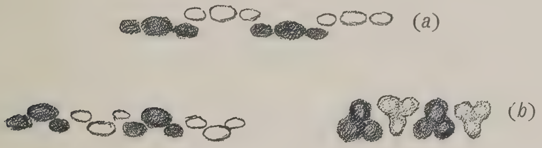

Fig. 206.

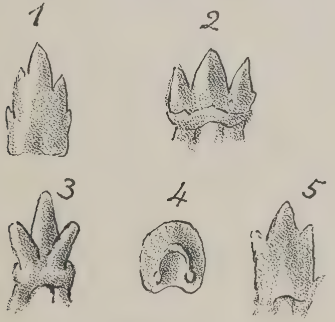

Fig. 207.

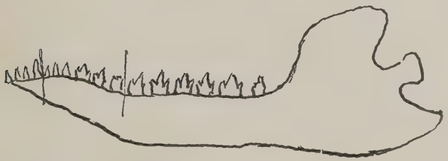

Fig. 205.—Diagram (after Cope) of upper (shaded) and lower (clear) teeth. (*a*) Stage reached in *Triconodon*. (*b*) Stage of ideal tritubercular teeth approached by *Menacodon*.

Fig. 206.—1. Tooth of *Dromatherium*. 2. Tooth of *Triconodon*. 3. Tooth of *Spalacotherium*, inner aspect. 4. Working surface. 5. Outer aspect. (After Osborn.)

Fig. 207.—Lower jaw of *Amphilestes*, from the Stonesfield slate, × 2. (After Owen.)

It is found that in the very generalised form, *Dromatherium*, the teeth are little more than simple cones ; in *Amphilestes* there is a triconodont stage ; while in *Spalacotherium* the three cones, instead of being placed in a line, have become in the upper teeth two outer and one inner, and in the lower one outer and two inner cusps.

At this stage we have the tritubercular tooth, and the teeth of the upper and lower jaws alternate with one another like the teeth of a dolphin (Fig. 190), an arrangement which with slight modification is exceedingly common in the mammals of the early geological periods.

The next stage in complexity consisted in the addition to the primitive triangles (trigons) of the posterior heel (talon), which carried a fourth cusp (hypocone). Such a tooth is termed trituberculo-sectorial, and was quite common amongst the Creodonta, and indeed other early mammals. The added heel in the lower teeth may carry another cusp besides the hypocone, to which the name entocone is given, whilst the upper teeth often have two additional cusps styled protoconule and metaconule.

So far the hypothesis commends itself by its simplicity as a generalisation, and indeed the convenience of having distinctive names for corresponding cusps, when that correspondence can be determined, is so great that the terminology is very commonly employed, even by those who hesitate to adopt the theory in its entirety.

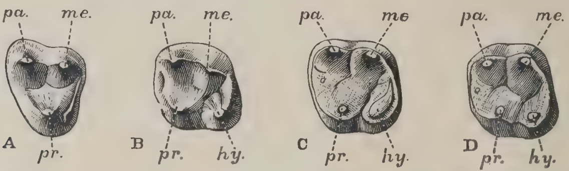

Fig. 208.—Upper molars of Primates, *Anaptomorphus* to *Homo*, showing evolution of the hypocone from the cingulum. A. *Anaptomorphus*. B. and C. Other Primates. D. Man. (After Osborn.)

The stages of trituberculism, a term first employed by Rutimeyer, are thus set forth by Osborn :—

I. a. Haplodont Type.—A simple conical crown, with single root, not well marked off from the crown. Not as yet known among primitive mammalia.

b. Protodont Type.—One main cone with lateral accessory cuspules ; root grooved. Ex. *Dromatherium* from American Trias.

II. Triconodont Type.—One central cone with two lateral accessory cones ; root double. Ex. *Triconodon*.

III. Tritubercular Type.—Crown triangular with three main cusps, the central or principal cone internal in upper molars and external in lower molars. Ex. *Spalacotherium* and *Asthenodon*.

IV. Trituberculo-sectorial Type.—Ex. Some living carnivores.

In these various sub-types the primitive triangles form the main body of the crown, to which other secondary cusps have been subsequently added.

By this means the teeth no longer wholly alternate, but some portions of them meet by their working surfaces. Nevertheless the alternation of that part of the teeth which is constituted by the primitive triangles remains, so that each triangle is opposed not by another, but by the added portion of the tooth, the talon of one falling into the hollow of the opposing trigon, the protoconule and metaconule always appearing at the spot where the talon abuts upon the trigon.

When, however, it is sought to apply the theory to more complex teeth, difficulties arise, and it even appears that in the upper and lower teeth of the same animal the subsequent additions of cusps do not follow the same order, and their homologies become doubtful.

The cusps of the primitive triangle may not all persist, even though other cusps are being added. Thus the formation of a quadritubercular tooth is often arrived at, not by the simple addition of one cusp to the primitive triangle, but by the addition of two and the more or less complete suppression of one of the three of the primitive triangle.

Thus the following tables represent the names given :—

Cusps of Lower Molars.

Primitive Triangle.
Antero-external = protoconid.
Antero-internal = paraconid.
Intermediate (or after the loss of the paraconid antero-internal) = metaconid.

Postero-external = hypoconid.
Postero-internal = entaconid.

Cusps of Upper Molars.

Primitive Triangle.
Antero-internal = protocone.
Antero-external = paracone.
Postero-external = metacone.

Postero-internal (sixth cusp) = hypocone.
Antero-intermediate = protoconule.
Posterior intermediate between metacone and hypocone = metaconule.

According to Osborn, the cusps of human molars are identified as follows :—

Lower Molars.

Antero-buccal = protoconid
Antero-lingual = metaconid
Trigon.

Postero-buccal = hypoconid
Postero-lingual = entaconid
Postero-mesial = hypoconulid
Heel.

Upper Molars.

Antero-palatal = protocone
Antero-buccal = paracone
Postero-buccal = metacone
Trigon.

Postero-palatal = hypocone—Heel.

The evolution of the human upper molar from *Anaptomorphus*, an

Eocene lemuroid, is illustrated in the foregoing figure after Osborn (*American Naturalist*, 1897, where a particularly clear summary of trituberculy is given) :—

"The talon or talonid always appeared first in the lower molars, and as it increased in dimension other cusps came in, so that in Lower Eocene mammals the lower teeth generally bore six cusps : the protoconid, paraconid, and metaconid in the trigon and the hypocone, hyperconulid, and entaconid on the talon." Thus, to borrow Osborn's words, "it was ready for transformation into the molar of a primate, an ungulate, or a carnivore, as the case might be."

To further illustrate the application of this nomenclature, taking the lower teeth, the lower carnassial tooth of the carnivora has the primitive triangle, with connecting ridges and an additional low hypocone. The same type occurs in many marsupials and insectivores (see Fig. 204).

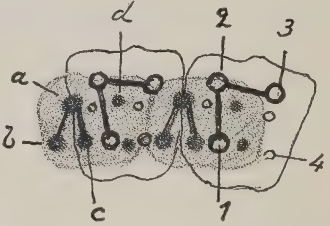

Fig. 209.—Diagram of two upper and two lower molars, adapted from Osborn in order to show relation of cusps. The shaded lower molars are supposed to be transparent, and to be looked at from below. The cusps of the primitive triangle are marked heavily, and are united by strong lines, those of the lower being solid, those of the upper ringed. *a*. Protoconid. *b*. Paraconid. *c*. Metaconid. *d*. Hypoconid. 1. Protocone. 2. Paracone. 3. Metacone. 4. Hypocone.

Add the hypoconid and entaconid to the primitive triangle, and we have a common type of quinquetuberculate molar ; then suppress one of the cusps of the triangle (the metaconid in Carnivora or the paraconid in Ungulata), and we get the quadricuspid bunodont molar. Or, to express it in other words, the divergencies occur in the direction towards bunodont teeth, in which a quadritubercular form is assumed by the loss of one of the primary cusps and the addition of a heel which contains two secondary cusps, or otherwise towards a sectorial type in which the heel is low, and the three primary cusps are connected by cutting ridges.

In the foregoing diagram an attempt is made to show the relations of the different cusps in upper and lower molars of a bunodont type. The alternation of the primitive triangles is well seen, as also the position of the hypocone and the other additional cusps.

Such is in brief the doctrine of trituberculism, the terminology of which has gained currency in most recent literature. For the present the determination of the homologies of the cusps set forth by Osborn still retains some hold, though it will most probably come to be modified in the future ; for this reason, in the later part of this book little attempt has been made to give these homologies in describing the teeth of individual mammals.*

Secondary, or Mesozoic.	Triassic— Lower, upper	First appearance of mammals, *Dromatherium*, *Microlestes*.	
	Jurassic— Liassic, Oolitic	*Ctenacoda*, *Plagiaulax* and other Multituberculates, Triconodonts and Trituberculates.	
	Cretaceous— Lower, upper	Multituberculates and Trituberculates, Marsupials.	
Tertiary, or Cainozoic.	Eocene— Lower . .	*Polymastodon.* Ancient types of Ungulata, Carnivora, Insectivora, Lemurs, Creodonts, Condylarthra.	Extinction of Multituberculata.
	Middle . .	*Hyracotherium*, Dinocerata, *Phenacodus*, Insectivora, Chiroptera, Hyracoidea, Artiodactyl and Perissodactyl Ungulates, Rodents, Fish, Lemurs, and Monkeys, Creodonts.	Condylarthra, Tillodonts, Dinocerata, some Creodonts.
	Upper . .	Creodonts, *Mesonyx*, Oreodons, Tapirs.	
	Miocene— Lower . .	*Mesohippus*, Creodonts, pure Dogs and Cats, Monkeys, Pigs and Peccaries, Opossums, Insectivora, Rodents, Creodonts, *Oreodon*.	Titanotheres, Hyracodon.
	Middle . .	*Miohippus*, Two-horned Rhinoceros.	
	Upper . .	*Protohippus*, *Hipparion*, *Mastodon*, Edentates, Rhinoceros, Deer, Llamas and Camels.	Creodonts, *Hyænodon*, *Oreodon*.
	Pliocene . .	*Equus*, *Mastodon*, Sloth, *Hyænidæ*, *Mustelidæ*.	
Post-tertiary or Quaternary.	Pleistocene .	Mammoth, Horse.	
	Recent . .	Man.	

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* Though the terminology is still retained, the number of adherents to the implied doctrine is steadily diminishing ; indeed, it seems doubtful if Professor Osborn is as ardent a supporter as formerly.—H. W. M. T.

It may save repetition and assist the reader not familiar with geology to give a table (p. 341) presenting the classification generally in use, leaving out the older formations in which mammals do not occur. The names of some of the actual forms alluded to are placed opposite their respective periods.

The earliest mammalian dentitions known to us carry us back no further than Mesozoic times, and of the Mesozoic mammals we may say that they had mostly smooth cerebral hemispheres, no inflection of the angle of the lower jaw, and forty-four or more teeth. Of these the canines had two roots, and the premolars and molars were little differentiated from one another.

If we except the Multituberculata to be presently described, all the teeth of the Mesozoic mammals are in some stage of trituberculism; indeed, this applies also to the early Eocene (Tertiary) mammals.

Of the few mammals known to have existed in Mesozoic times, about a dozen genera have been obtained from a single locality: the Purbeck bone bed. This is a fresh water deposit found near to Swanage, and it is no larger than the floor of a very moderate-sized room, and only six inches deep. From this tiny patch comes most of our record of English Mesozoic mammalia, and in it are forms so differentiated, as, for example, *Plagiaulax*, as to clearly indicate that at this date mammals had long existed and were present in the country in great numbers, yet we know nothing at all of them.

A considerable number have been found in Wyoming in Jurassic formations, and the late Professor Marsh, pending evidence which would place them either amongst the Metatheria or Eutheria, proposed for them the provisional orders Pantotheria and Allotheria.

He considered that his Pantotheria were probably placental, and his Allotheria, which had fewer teeth, greater specialisation of the premolars and molars and an inflected angle to the lower jaw, were probably marsupial mammals, but he infers from what is known of the earliest mammals that the placentals are not descended from the marsupials, but that both have arisen from a common stock, perhaps of Monotreme character.

The American Mesozoic mammals, known only by teeth and jaws, were very similar to the European forms.

The dentition of *Amphitherium*, of which the lower jaw only has yet been found, is one of the earliest known. It was obtained from the Jurassic formations; sixteen teeth were present, which, so far as their forms can tell us, were

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Of Mesozoic mammals in general, it may be said that the earliest are known by isolated jaws, or even by a few detached teeth only, but those coming a little later are better known, largely by the magnificent finds which have rewarded the American naturalists.

A large series of early mammals have come from the Puerco beds of New Mexico, which are either Eocene Tertiary, or even a little earlier (Osborn and Earle (7)). They are remarkable for the large number of orders represented, from the multituberculate allies of *Plagiaulax* to representatives of the Primates, which appear already to have been both abundant and specialised.

No bunodont forms occur in the Mesozoic period, but they are first met with in the Cretaceous period. The early and very general assumption of the tritubercular type indicates that the simpler forms are to be sought outside the mammalia, and it suggests that where we find them in mammals they may be due to retrogression.

One prevalent type of Mesozoic mammals resembles somewhat the polyprotodont marsupials; there are three or more lower incisors, the canines are pronounced, and the cheek teeth are cuspidate, reaching in some cases the number of twelve. But it is uncertain whether they were really marsupials.

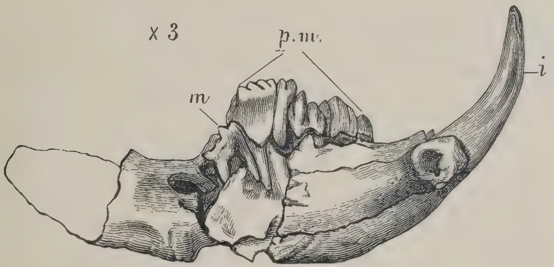

FIG. 210.—Lower jaw of *Ctenacodon*. (After Marsh.)

Another type of mammals, termed Multituberculata, on account of the many tubercles which their molar teeth present, appeared in Mesozoic times and extended on into the Puerco beds.

They may be provisionally divided into two groups, one of which includes *Polymastodon* and its allies, and the other comprises *Plagiaulax* and allied forms. It must not be inferred that they were necessarily marsupials; indeed, some writers consider them to have possibly been Monotremes. Professor Marsh has described several Mesozoic forms like *Plagiaulax*, but upper and lower jaws not having been found together *in situ*, it is somewhat problematical which upper belongs to which lower jaw.

The lower jaw of one of these, to which the name *Ctenacodon* has been given, found in strata of Jurassic age, has a single long pointed incisor, four compressed cutting premolars, and two minute tubercular molars behind them.

They are so strongly differentiated that they cannot be regarded as ancestral types, and the manner of succession reminds us of that seen in marsupials. The *Plagiaulacidæ* have compressed cutting premolars resembling somewhat those of *Hypsiprymnus*.

A great controversy once raged as to the probable diet of these forms.

Professor Owen, basing his arguments largely upon the presence of premolars which possessed elongated and sharp-edged blades, held that *Plagiaulax* was carnivorous, saying that it possessed an effective dental machinery for predatory life; Dr. Falconer and Sir W. Flower have shown this view to be untenable, or at least unsupported by adequate evidence.

Professor Marsh remarks that all the mammals older than Tertiary times may have been insectivorous, but that *Plagiaulax* shows an adaptation to some special food, whether animal or vegetable is as yet unknown.

The true molars do not, however, resemble those of existing marsupials; on the other hand, the angle of the lower jaw is inflected as in them.

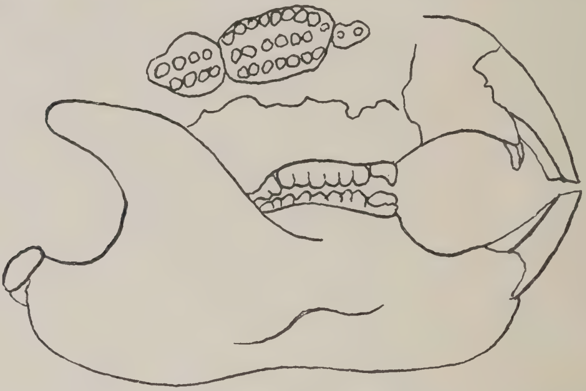

Fig. 211.—Dentition of *Polymastodon*. (After Osborn.) The grinding surfaces of the multituberculate upper molars are shown separately.

Polymastodon (Cope), besides being possessed of multituberculate molars (there are no less than twenty-eight oval cusps upon the first upper molar), had two long slender rodent-like incisors in both upper and lower jaws, with the enamel confined to the anterior surface; in the upper jaw there were in addition two small incisors. In the lower molars there were normally only two rows of cusps, though occasionally signs of an additional row are present.

Upon the existence of these teeth has been based yet another theory of the genesis of mammalian teeth, viz., the multitubercular or polybuny theory, upheld by Forsyth Major (⁴). It has been pointed out by him that amongst the earliest mammals known to us are some which were not tritubercular, but multitubercular, and that there is just as much ground for supposing that the tritubercular tooth, when it does occur, has been arrived at by a process of reduction in cusps, as that it is derived from a triconodont type. And

Ameghino cites *Proteodidelphys*, an ancient form (Lower Cretaceous), as possessing six cusps with indications of others. Hence he regards six cusps as a primitive form, and any smaller number as being a reduction. This brings us to a consideration of some of the difficulties which stand in the way of the tritubercular theory.

Some authorities differ in the determination of the homologies of the cusps. There are those who strongly dissent from the proposition that the protocone is on the inside in the upper teeth, holding that it is on the outside in both upper and lower teeth. Again, Scott (9) considers that what is true of the molars is not true of premolars, claiming that even where the premolars attain to a close resemblance or identity with the molars, yet the resemblance is superficial, and that it has been arrived at by a different process, the protocone in them being on the outside in both jaws.

He proposes for the premolars a slightly different nomenclature, namely, protocone, deuterocone, tritocone, tetracone, in the order of the successive appearances of cusps in the palæontological series. If this could always be ascertained, this nomenclature would seem an improvement, but the imperfection of the geological record renders this not always possible.

He considers that the internal cusps of premolars have been derived from elevations of the cingulum, and not from any ancestral tritubercular cusp. To this view Cope lends some support, remarking that we "seem to have here an excellent illustration of the origin of two identical structures by different evolutionary routes," rather than regarding it as a difficulty in the acceptance of the theory generally.

[It is still an open question whether the premolars have or have not followed the same order of cusp evolution as the molars. In the older Cope-Osborn (tritubercular) theory it was held that the evolution was different in the two series, but now, in what Osborn terms the "newer theory" (5c), the opposite conclusion is maintained. This is termed the "Premolar Analogy Theory," which holds that "the superior molars originally acquired trituberculy in a manner similar to that which can be traced in the premolar metamorphosis." This idea was first suggested by Huxley in 1880. It is supported by Schlosser, and by Wortman and Gidley on palæontological grounds. It would appear that both embryology and palæontology furnish evidence in support of the view that the antero-external cusps of the upper molars represent the primitive reptilian cone.

Marett Tims' views are a slight modification of this (10b). He believes that the course of evolution of the molars and premolars was originally the same, but that in the case of the former an antero-posterior concrescence of the teeth has taken place, so that in reality both external cusps of the molars represent the reptilian cones of originally separate cheek teeth. The internal and subsidiary cusps he derives from that archaic structure the cingulum. In this way one of the great objections to the Cope-Osborn theory, viz., the implied rotation of cusps in the evolution of the tritubercular from the triconodont pattern, is avoided.]

Another stumbling-block has been pointed out by Marett Tims (10a) in the acceptance of the tritubercular theory. It would be in accordance with other facts in development if the primitive cusp, even though in the adult it was going to be reduced in size below the others, should be the first to appear in the course of development. But it happens that in some Primates, Marsupialia, Ungulata, Insectivora, Rodentia, and Canidæ, this is not the case : the protoconid does, but the protocone does not, develop first; and in some it is even not the second to appear, the paracone always, and the metacone usually, appearing in the tooth-germ before it.

With the exception of two insectivores, *Centetes* and *Ericulus* (and some doubt is thrown even on these), in all animals which have been adequately examined the paracone and the protoconid are the first to appear ; the evidence of ontogeny therefore points to these being homologous cusps, they being in each instance the antero-external cusps. This may seem a small matter, but if the reversal of the primitive triangle (cf. p. 337) does not take place, this initial and, from the point of view of the theory, very important stage is a fallacy.

Whilst Osborn points out that antagonism would lead naturally to the longest (protocone) cusp being on the inside in the one jaw and on the outside in the other, this functional adaptation does not help much to establish the homology of these longest cusps with one another.

Marett Tims further points out that the majority of the fossil forms, on which the tritubercular theory is chiefly based, occur in strata not very different in age, and that to him at least the evidence of palæontology is as deficient as that of embryology is damaging. But whatever the ultimate fate of the theory may be, morphologists will always owe a debt of gratitude to its advocates in that they have studied, and induced others to study, the evolution and homologies of the cusps with an accuracy which would in all probability not have been attempted but for the theory, and have reduced to order the nomenclature * and the history of the evolution of the complex teeth of ungulates, which were previously in a chaotic condition.

[In a series of papers, the outcome of prolonged and extensive researches, Bolk has propounded a new theory to account for the origin of the patterns of the teeth in the mammalia, and which he calls the "Dimer Theory." It is difficult to do adequate justice to his views in a short summary, but the main points may be given, more or less in his own words. The complete theory is based on four theses or hypotheses (^{2b}) :—

1. *The Hypothesis of Triconodonty.*—It is affirmed that the reptilian tooth from which that of mammals was evolved was not of a haplodont type, but triconodont. The conical tooth of the Crocodilia is not a primitive form, but derived secondarily from a

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* The reduction to order here referred to is unfortunately now again reduced to disorder. The terms protocone, &c., may still be used to denote certain cusps, but certainly not with an assured implication of morphological significance, such as was intended when the terms were first adopted.—H. W. M. T.

tooth compressed from side to side and with a sharp cutting edge. Such a form of tooth is to be found in the embryo of *Crocodilus porosus*, but which neither cuts the gum nor is functional. It is also frequently met with in other reptiles, *e.g.* lizards, as well as in the extinct Cynodontia.

2. *Hypothesis of Dimery.*—Every mammalian tooth, with certain exceptions, is homologous with two reptilian teeth, the outer series of cusps of the molars and premolars representing one reptilian tooth and termed the *protomere*, the inner series a second tooth and named the *deuteromere*, each longitudinal half of the two forming a single odontomere which is thus monomerous. The existence of the *tuberculum impar*, or tubercle of Carrabelli, a minute tubercle occasionally present on the inner face of the internal cusps, Bolk regards as an abortive attempt at tritomerism. The mammalian tooth-germ is thus not the homologue of one reptilian tooth-germ, but of two. The complete tooth-germ of the mammal is really a duplicate organ. The double nature of the tooth-germ is evidenced by the double connection of the enamel-organ with the epithelial lamina from which the teeth are developed, by the two centres of pulp formation (*vide* Chapter V). This latter is confirmed by Ahrens, who states that at an early stage of tooth development the layer of ameloblasts is divided into labial and buccal portions by the enamel septum being continuous with the apex of the dental papilla.

3. *Hypothesis of Concentration.*—In the development of the reptilian teeth, Bolk regards an individual tooth and its numerous successors as a "tooth family," one tooth generation succeeding another with more or less prolonged intervals. In the mammals the power of producing numerous generations (*i.e.* polyphyodontism) is much reduced, and the intervals much shortened. As a consequence there is a concentration of the anlage of two reptilian teeth to form one mammalian tooth. Bolk distinguishes between concentration and concrescence.

4. *Hypothesis of Equivalence.*—The elements of a mammalian set of teeth are all morphologically and genetically equivalent. The terms mono- and multi-cuspidate possess only a descriptive anatomical value and do not indicate any morphogenetic differences. The differences in shape are solely of a quantitative nature. The anlage of every tooth possesses the potentiality of developing all the cusps found in the most complicated tooth of the set. "Complication is to be regarded as completeness." Simplicity of a tooth is explained by the fact that the anlage of a tooth develops its potentialities in a more or less incomplete manner.

Such then is the main outline of Bolk's Dimer theory. From the foregoing it is clear that, according to this view, the fundamental type of a mammalian tooth is sexitubercular, the protomere and deuteromere each representing a triconodont reptilian tooth, the central cone in each being the most pronounced. This conception has led Bolk to introduce a most convenient method of indicating the cusps, for which all workers at the subject will be very grateful.

A sexicuspidate tooth is indicated by the formula

$$\frac{1P2}{1D2},$$

the main cone of the protomere and deuteromere being indicated by capital letters, and the anterior and posterior cuspules by small numerals. If the latter should fuse with the former, such a condition is indicated by $\frac{P}{D}$, *i.e.* a bicuspid type of tooth. If the main cone be subdivided into two, as in the molar teeth of man and many mammals, this is shown by the formula

$$\frac{a\ \ P\ \ Pp}{a\ \ D\ \ Dp}.$$

To the above account of the evolution of the mammalian molars and premolars Bolk regards the teeth of the Multituberculata and Proboscidea as partial exceptions (^{2a}). Whereas the bulk of the mammalia are dimerous, these animals are polymerous. An elephant's molar represents not merely two generations of a tooth family, but the whole family of at least ten generations, the anterior lamellæ representing the oldest generation and the posterior the youngest, the relative positions of the generations as compared with other mammals being due to a rotation of the tooth-germ in the jaw of the fœtal elephant, of which Bolk thinks he has found evidences (*vide* p. 485).

The ordinary type of mammalian incisors and canines are regarded as forms in which the deuteromere is much reduced but is still visible in the thickening to be observed near to the cervical border of the lingual surface.

The main cusp of these teeth, as is well known, often shows a triconodont pattern, interpreted by Bolk as a retention of the primitive triconodont protomere. In this light heterodontism is due to the variable development of the deuteromere. Haplodontism is a secondary condition, whether occurring in Odontocetæ or in Crocodilia.

The theory of dimerism, though it has much to recommend it, must still be regarded as *sub judice.* Numerous papers by Adloff have appeared in the *Anatomischer Anzeiger* attacking various aspects of the theory. Should it turn out to offer a correct interpretation of the facts of mammalian tooth morphogenesis, many of the now accepted views would necessarily fall to the ground.]

Besides the introduction of new cusps, the pattern of a tooth may be complicated by infoldings of its surface, whether on its sides or on its apex.

If we take a simple conical tooth with one cusp, such as a canine, and grind or wear down its apex till the terminal portion of enamel is removed, its blunted end will present a more or less circular area of dentine, surrounded by a rim of enamel. If we imagine a tooth with four long similar cusps, we shall at a certain stage of wear have four such areas, while eventually, as the tooth gets worn down below the level of the bases of the cusps, there will come to be a single larger area of dentine surrounded by enamel. Thus in those teeth the grinding surfaces of which are rendered complex in pattern by the presence of several cusps the pattern changes from time to time as the tooth wears down ; while the addition of thick cementum, filling up the interspaces of the cusps, adds a further element of complexity, as is seen in the teeth of most herbivorous creatures. The change of pattern induced by the wearing down of the surface to a lower level is well and simply illustrated by the " mark " of the incisor teeth of a horse.

Fig. 212.

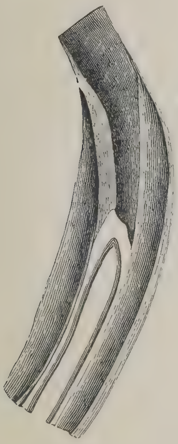

Fig. 213.

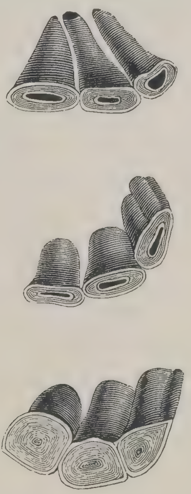

Fig. 212.—Horse incisor, longitudinal section.
Fig. 213.—Horse incisor, showing the mark at various ages.

In an uncut, and therefore perfectly unworn tooth, the condition of the apex may be compared to the finger of a glove the tip of which has been pushed in or invaginated. The depression so formed is, like the rest of the surface, coated with enamel, and with a thin layer of cementum. When the tooth is worn down to a considerable extent there is a field of dentine, in the centre of which is an oval ring of enamel, within which is a space filled with the *débris* of food, &c. This constitutes the " mark," and as the tooth becomes further worn down, below the level of the bottom of the pit, the " mark " disappears, and a plain area of dentine results.

Somewhat similar inflections occur abundantly also upon the sides of teeth. The inflection of the surface, which in the incisors of the horse is of the simplest possible form, may be cruciform or variously waved and broken up, thus leading to all sorts of complications of surface. As the tooth becomes worn, the longitudinal inflections, running in from the sides, may also be oblique or variously waved, or they may extend through the entire width of the tooth, thus cutting it into a series of plates of dentine and enamel, fused into one tooth by the cementum. (See Fig. 217.)

A common pattern of tooth is formed by the junction of the two anterior and two posterior cusps by simple ridges ; and the cingulum may connect the outer ends of these two ridges ; such a tooth is seen in the tapir, and in *Palæotherium.* By the varied obliquity of these ridges, and by the introduction of secondary inflections, patterns apparently dissimilar are arrived at.

In the molar teeth of the horse, arrived at by a modification of the Palæotherium type, we have a surface constantly kept rough by the varying hardness of its different constituents.

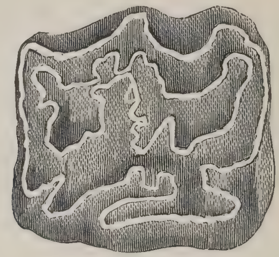

Fig. 214.—Molar tooth of horse, showing the characteristic pattern of its grinding surface.

In a worn tooth there are two islands of cementum upon a general field of dentine bounded by tortuous lines of enamel, and on the inner side a sort of promontory of dentine, bounded by enamel. The tortuous lines of enamel by virtue of their hardness will, at all stages of wear, be more prominent than the dentine or the cementum, and will hence maintain the efficiency of teeth as grinders.

The patterns of grinding surface thus produced are very constant for allied species, so that an individual tooth of a herbivore may sometimes be correctly referred to its genus and always to its family.

But as it will be necessary to recur to this subject from time to time, and especially in connection with the Ungulata, it will suffice for the present to point out that such correspondences do exist, and that all the complexities of pattern found may, in practice, be to some few types.

The development of additional cusps from upgrowths of the cingulum, and the suppression or fusion of pre-existing cusps, may be traced by a comparison of the teeth of allied animals, and thus connecting links are found between patterns at first sight very dissimilar. The order Proboscidea affords, however, so instructive an instance of the manner in which an exceedingly complex tooth has been derived from a simple one, that it may be mentioned in this place as an example.

The tooth of the elephant is so strikingly unlike other teeth, that it might at first sight be supposed that it is more essentially different than is really the case. The clue to its nature is afforded by the teeth of an extinct Proboscidian, the *Mastodon*. If the second true molar of one of the mastodons (*Tetralophodon*) be taken as a starting point its crown is found to be made up of four strongly pronounced transverse ridges, the summits of which are made up of rounded eminences (whence the name *Mastodon*, from μαστός, a nipple). The four transverse ridges coalesce at their bases, and the crown is supported upon a number of roots corresponding to the ridges.

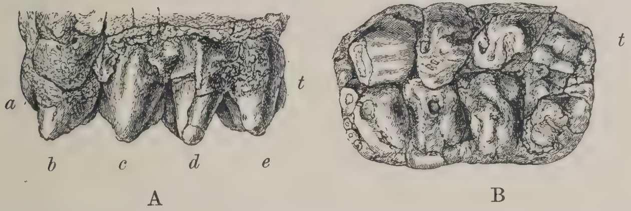

Fig. 215.—Second upper molar of *Mastodon* (*longirostris*), from Falconer. A. Side view. B. View of the crown surface. About one-eighth natural size. The four transverse ridges, *b*, *c*, *d*, *e*, are seen to be, to some extent, divided into outer and inner cusps by a longitudinal cleft, much less deep than the transverse indentation. At the front there is a slight elevation of cingulum into a "talon" (*a*), and a similar one at the back of the teeth; by its further elevation additional ridges or cusps might be formed.

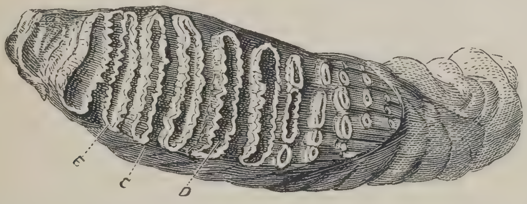

Fig. 216.—Molar tooth of an Asiatic elephant, showing the transverse plates of dentine bordered by enamel: *c*, cementum; *d*, dentine; *e*, enamel.

If we take the next tooth, or the third true molar, the general character remains the same, except that there are five ridges, and indications of as many roots; still the general correspondence of the ridges with the cusps of less aberrant teeth is obvious. The crown is coated by enamel, over which there is a thin layer of cement, which does not fill up the whole interval between the ridges. Thus the tooth, though very large, is not a very aberrant one; it is obviously nothing more than a tooth in which the somewhat numerous cusps are connected by transverse ridges, and are very long and strongly pronounced.

To convert the tooth of a mastodon into that of an elephant, we should have to multiply the number of ridges,* to further increase their depth, to fill up solidly the interspaces between them with cementum and to stunt the roots. The completed tooth of an elephant is a square or rather oblong mass, from the base of which spring contracted and stunted roots. It consists of a common pulp cavity, small in proportion to the bulk of the tooth, and deep down in the mass; from it many thin laminæ are sent up towards the surface, each forming the core of an area of dentine enclosed by enamel; and the interspaces of these exaggerated cusps are solidly filled in by cementum.

Between the *Mastodon* and the Indian elephant are a number of transitional forms in which we are able to trace the gradual modification of the not excessively aberrant tooth of the *Mastodon* into the very peculiar huge molar of the Indian elephant. And Andrews has recently found in Miocene formations in Egypt forms which illustrate the evolution of the Proboscidea from less aberrant mammalian types.

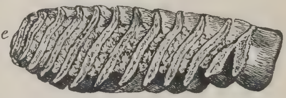

FIG. 217.—Molar of Capybara, showing the transverse plates of dentine and enamel united to one another by cementum.

The numerous transverse plates of the elephant's grinders are united by dentine at their bases, and a common pulp cavity and truncated roots are formed; but in this last respect the molar teeth of the Capybara depart still further from the ordinary type, for, being molars of persistent growth, their numerous transverse plates of dentine and enamel do not become continuous, and there is no common pulp cavity. It is as though in an elephant's grinder the plates, which are for a long time distinct, never coalesced, but continued to grow on separately, being united with their fellows by cementum only. Further differences may be due to the partial or complete absence of one or another of the constituent tissues.

[Bolk has recently examined a fœtal elephant 20 cm. long (2c). The interpretation which he has put upon the evolution of the tooth pattern of the Proboscidea as a result of his extensive researches into the tooth genesis of the mammalia, and in his opinion corroborated by what he found in the fœtal jaws, is briefly as follows: The tooth of the elephant is "polymerous," a single tooth representing a whole "tooth family" of the reptiles, the oldest generation of which is represented by the anterior lamella of the tooth and the youngest by the posterior lamella, this antero-posterior position of the succeeding tooth generations being brought about by a rotation of the tooth-germs as they develop, and of which he believes there is evidence in the fœtus which he has examined.]

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* This multiplication of the ridges may be explained by an antero-posterior fusion of originally separate teeth (10b).—H. W. M. T.

In what might be termed a typical tooth there should be a single axial pulp cavity surrounded by hard dentine, this again being capped over the crown by enamel and entirely invested by cementum.

The layer of coronal cement may be absent, as in man or the Carnivora; or the investment with enamel may be only partial, as upon the front of a rodent incisor, or on the tusk of a pig or *hippopotamus;* or a tooth may be composed solely of a mass of hard unvascular dentine, coated with cementum, as in the tusk of an elephant.

And just as endless varieties of teeth may be produced by the suppression, or partial suppression, of certain of the tissues, so differences may be brought about by the occurrence of other than the three usual tissues. Thus the remains of the central pulp cavity often become occupied by calcified pulp, forming "osteo-dentine"; this, which occurs in man as an almost pathological condition, is perfectly normal in many animals, in the sperm whale, for instance, or in the constantly growing teeth of the sloth, the central axes of which are occupied by dentine permeated by vascular canals.

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CHAPTER XIV.

THE TEETH OF MAMMALIA—PROTOTHERIA.

THE ancestry of the mammalia remains still somewhat uncertain, and the theriodont reptiles are possibly not in the direct line of descent, though they present certain resemblances to mammals, and are perhaps not far from the stem.

The mammalia are usually now divided into three groups—**Prototheria, Metatheria,** and **Eutheria.**

The **Prototheria** comprise numerically but few animals, as no extinct forms are known with any certainty, and of living animals only two families exist, namely, the *Ornithorhynchidæ* and the *Echidnidæ.*

They stand at the bottom of the mammalian class, and present many points of affinity with lower vertebrates, particularly with Sauropsida and Amphibia.

Metatheria, like the preceding group, have characters which place them low in the mammalian scale. They are numerously represented at the present day, comprising the animals known as marsupials, which practically monopolise the Australian region, but exist also in the South American continent. In former times they existed over other portions of the globe, and some of the earliest mammalian fossils are perhaps referable to the group.

Eutheria comprise all the mammals in which the young are nourished by means of an allantoic placenta.

It must not be supposed by the student that the Metatheria of the present day are descended directly from the Prototheria, or that the Eutheria are direct descendants of the marsupials. It is more probable that exceedingly early and unknown mammalian forms have given rise to each of these stems, and that the Prototheria have advanced but little, the marsupials a good deal, giving rise to a large number of forms, while the Eutheria have far outstripped the others, and have been and are supplanting them in all directions.

PROTOTHERIA.

The *Echidna*, or Scaly Ant-eater, is, so far as is known, entirely edentulous at all stages of its growth. Its palate and tongue are, however, beset with hard spines.

The *Ornithorhynchus*, which in its soft parts and skeleton alike differs from higher mammals in points which approach the characters of Sauropsida, is furnished with wide flattened jaws, in which horny plates fulfil the function of true teeth ; from this peculiarity comes its name of duck-billed platypus.

Caldwell discovered that, though possessed of functional mammary glands, it lays eggs, and subsequently Professor Poulton in 1888 (1) found that at an early stage tooth-germs were present, as he supposed, underneath the horny plates. Following upon this, Oldfield Thomas found that its true teeth came into actual use, and that they were not beneath but superficial to the horny plates.

To take first the dentition, if such it can be called, of the adult animals, the horny plates with which the jaws are ultimately furnished are four in number in each jaw, the anterior plate being a thin long band with a longitudinal ridge and a furrow in its inner side, and the posterior plate a flat, broad-topped mass, the surface of which is roughened by a series of ridges separated from one another by concavities, the ridges of the opposing plates interdigitating with one another.

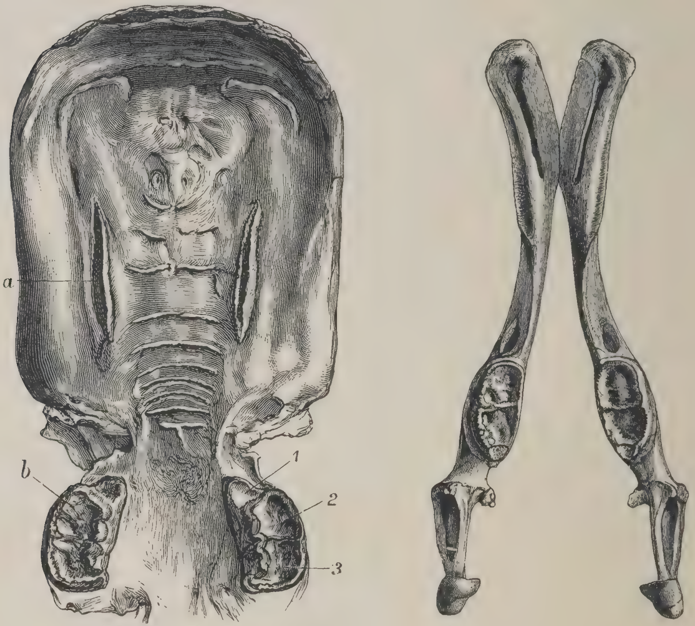

Fig. 218.—Upper and lower jaws of *Ornithorhynchus*. From the lower jaw the skin, &c., has been removed, but it remains upon the upper. *a*. Anterior horny plate. *b*. Posterior horny plate, with remains of tooth sockets, 1, 2, 3.

These plates are simply pronounced thickenings and hardenings of the oral epithelium, and their under-surfaces are penetrated by long papillæ, each of which sends up a prolongation of soft, deeply staining cells from its apex. The plates are at their sides quite continuous with the stratum corneum of the epithelium, of which their harder portions are composed ; there is no calcification, and no bony structure in them. Somewhat similar horny structures occur upon the tongue.

A full account of the structure and form of these plates will be found in a paper by Poulton (²), which is devoted to a full description of his most interesting and significant discovery of the existence of the true tooth-germs, which he then believed to underlie the forming horny plates.

Fig. 219.

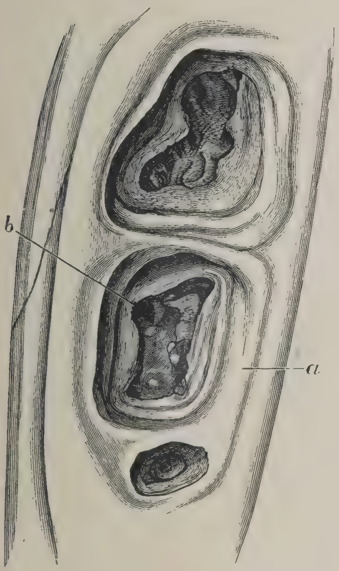

Fig. 220.

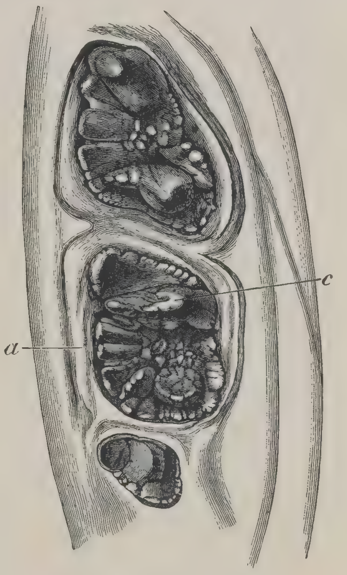

Fig. 219.—Horny plate, *a*, of a half-grown *Ornithorhynchus*, with empty pits, *b*, for the reception of the teeth.

Fig. 220.—Horny plate with teeth *in situ*. *c*. Long cusp of tooth. After Professor Stewart, from a specimen in the Royal College of Surgeons' Museum.

From want of material he was somewhat uncertain as to the extent to which the calcification of these teeth goes and what afterwards becomes of them, but he saw that there were the germs of four teeth in the upper on each side, and probably the same number in the lower jaw ; and they occupy a widely open furrow, which he thought was subsequently occupied by the horny plate.

[In a more recent paper by Professors Wilson and Hill (⁶) the tooth development in *Ornithorhynchus* has been described. In a young specimen 80 mm. in length, " each jaw shows two definite papillated enamel-organs," and in front of these a " calcified vestigial toothlet." In an older specimen with a length of 250 mm. there are present in each jaw "two very large enamel-organs, each with a number of calcified cusps," representing the two large multicuspidate teeth of the young adult, anteriorly to these in the upper jaw an enamel-organ with a single calcified cone, and still more anteriorly another rudimentary papillated enamel-organ. In the lower jaw, in front of the two large multicuspidate teeth, is a minute calcified tooth, while behind them is a well-developed uncalcified enamel-organ.

On comparison with the dentition of the young adult the authors conclude that in the two specimens which they examined there are "representatives of five quasi-permanent teeth" in each jaw, together with "vestigial representatives of deciduous predecessors to the most anterior of these five tooth-elements." The accompanying figure (Fig. 221) taken from Wilson and Hill's paper shows all these in a diagrammatic way, with the exception of the most posterior upper molar, which in these stages is only represented by a special thickening of the dental lamina.

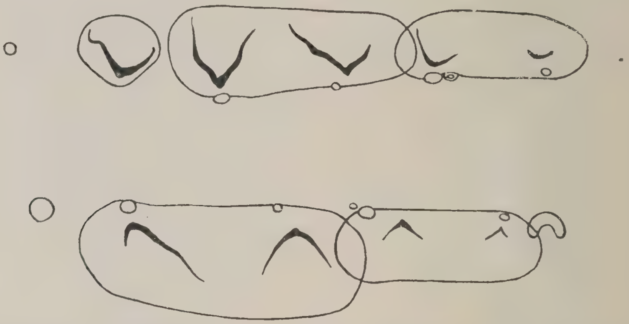

FIG. 221.—Schematic figure showing the actual tooth-germs in *Ornithorhynchus*. (After Wilson and Hill, Quart. Journ. Micr. Sci. Lond., vol. li., N.S., 1907.)

These observations are of very considerable interest, as they not only demonstrate the presence of two dentitions in the Monotremes, as had previously been surmised by Tims (5), but they also afford evidence of concrescence in the molar teeth.]

In this connection it is interesting to note that Professor Huxley, in writing of the Monotremes, had years ago expressed the conviction that there is good reason to suppose that edentulous forms are modified descendants of toothed forms.

Oldfield Thomas (4) and subsequently Professor Stewart (3) found that the true teeth of *Ornithorhynchus* are cut, and for a time are in actual use. They are twelve in number, two on each side being of some size, and the third very small. The upper teeth have broad-topped crowns, with two long cusps on the inner edge, and a crenated border along the outer edge with many small cusps; in the lower this is reversed. They have low broad crowns with short stunted roots, by which, however, they are for a time fairly firmly held. The crown pattern of these teeth are strikingly like those of the fossil *Microlestes*, as is shown in Fig. 222.

Instead of being beneath the horny plates, they are on the top of them, and their implantation is peculiar ; the expanded crowns narrow rapidly at the neck, and they are surrounded by a very dense and thick epithelium, almost horny, which rises into a ring round them and dips underneath the expanded portion, so that the tooth lies in a sort of cup of horny consistency.

This cup is not complete at the bottom, but the roots pass through it and fit depressions in the bone, which is perforated by foramina for their vessels and nerves. When the creature is about twelve inches long the teeth are shed, and then the horny cups grow in underneath and become complete. Thus the curiously cupped and sculptured surface of the horny plates which have been so long familiar has its form determined by once having formed the bed for a tooth with several roots, and although the horn grows underneath and fills up the holes for the roots to go through, yet the old general form is more or less maintained by the horny plate which serves as the organ of mastication throughout the rest of the life of the animal.

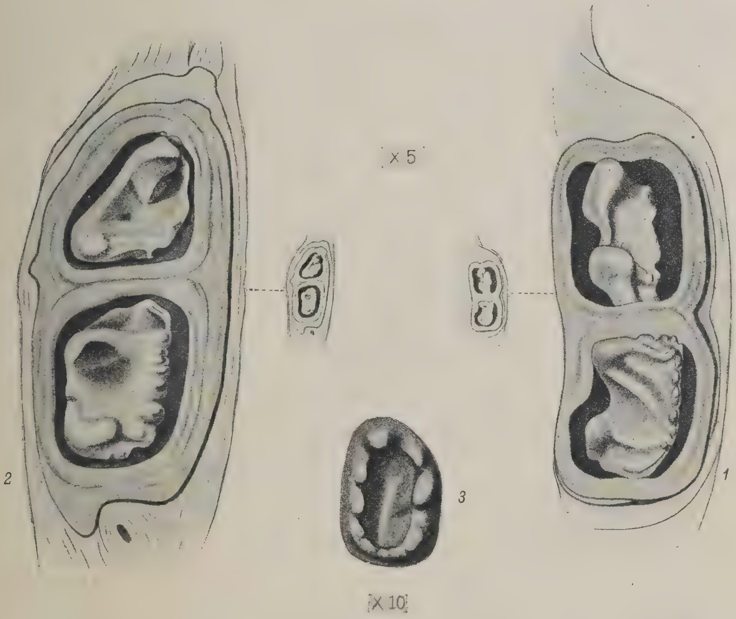

Fig. 222.—1. Left upper teeth of *Ornithorhynchus*. 2. Left lower teeth. 3. Molar teeth of *Microlestes*, much magnified. (After Oldfield Thomas, Proc. Roy. Soc. Lond., vol. xlvi., 1890.)

So far as is known, this is an arrangement quite unique amongst mammals, or indeed any other tooth-bearing creatures.

The horny plates are therefore not at all to be regarded as horny teeth, but they are epithelial structures which take the place of the teeth after these are shed, and therefore they are not absolutely similar to the horny teeth of lampreys and myxinoids.

The true teeth consist of a body of dentine, with a central pulp cavity, capped with thin but hard enamel, and implanted by short roots, the breadth of crown greatly exceeding its vertical dimensions.

The enamel is apparently of simple structure, and the dentine is permeated by fine dentinal tubes and beset with a wonderful number of interglobular spaces, which in parts of the crown mask its tubular structure. In the principal cusp larger, apparently vascular, canals exist, and as one approaches the stunted roots a somewhat abrupt transition in structure takes place, all dentinal tubes disappearing and large lacunæ appearing. The roots are hence of softer, coarser material than the crown, which itself is not of a high type of dentine structure.

Thus the dentine structure of the tooth is somewhat that which we are accustomed to see as a result of pathological processes, and would suggest, so far as it goes, that the *Ornithorhynchus* tooth has degenerated from some earlier and more complete tooth-form in which the roots consisted of properly developed dentine.

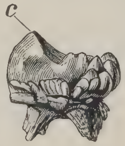

FIG. 223.—Molar tooth of *Ornithorhynchus*. c. Long cusp.

The author is not acquainted with an example of this degeneration in the type of dentine formation as the root portion of the tooth is approached in any other mammalian tooth. In those teeth which have no roots, if such an expression may be allowed, but which are about to become anchylosed to the bone, something of the kind may be seen. (Cf. also the tooth of *Hesperornis*, p. 304.)

The British Museum specimen described by Oldfield Thomas (*loc. cit.*)* shows that the teeth were subjected to severe attrition, as one, which was about to be shed, was worn as thin as paper. No tooth, fossil or recent, corresponds in naked eye characters with that of *Ornithorhynchus*, though that of the Mesozoic *Microlestes*, as has been already stated, does so in some degree.

Microlestes has generally been looked upon as a marsupial, allied to *Plagiaulax*, though Cope has suggested that all the group of multituberculate toothed Mesozoic mammals may have been Monotremes.

But a microscopic examination of a tooth of *Microlestes*, which

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* An interesting discussion on the significance of the teeth of *Ornithorhynchus*, by Professor St. George Mivart, will be found in the "Proc. Roy. Soc.," 1888.

Professor Poulton kindly allowed the author to make, shows no close resemblance to the recent marsupials, for the enamel is not clearly penetrated by dentinal tubes, nor does it present the peculiarities of structure found in *Ornithorhynchus*. Thus its structure gives no help, but rather goes to render still more indefinite its probable zoological position.

Though there is no doubt that the *Ornithorhynchus* reveals to us a tooth of a period very remote in point of time, it has yet by no means a simple crown, and it does not help us much towards knowing anything which can be regarded as a primitive parent form whence all mammalian teeth may have been derived.

Still the discovery is of incalculable value, inasmuch as many of the early mammalia are known to us only by teeth, and the form and structure of a monotrematous tooth gives us something far lower in the evolutionary scale than had hitherto been known.

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(2) ——————— "The True Teeth and the Horny Plates of *Ornithorhynchus*." Quart. Journ. Micr. Sci., 1889, vol. xxix., N.S., pp. 9—48.

(3) Stewart, C. "On a Specimen of the True Teeth of *Ornithorhynchus*." Quart. Journ. Micr. Sci., 1892, vol. xxxiii., N.S., pp. 229—231.

(4) Thomas, O. "On the Dentition of *Ornithorhynchus*." Proc. Roy. Soc. Lond., 1889, vol. xlvi., pp. 126—131.

(5) Tims, H. W. Marett. "The Evolution of the Teeth in the Mammalia." Journ. Anat. and Phys., 1903, vol. xxxvii., pp. 131—149.

(6) Wilson, J. T., and Hill, J. P. "Observations on Tooth Development in *Ornithorhynchus*." Quart. Journ. Micr. Sci., 1907, vol. li., pp. 137—165.

CHAPTER XV.

THE TEETH OF METATHERIA—MARSUPIALIA.

MARSUPIALIA	Polyprotodontia	*Didelphyidæ* *Dasyuridæ* *Notoryctidæ* *Peramelidæ*
	Paucituberculata	*Epanorthidæ*
	Diprotodontia	*Phascolarctidæ* *Phalangeridæ*

THE great sub-class of marsupials, consisting of animals sharply marked off from placental mammals by many striking peculiarities, amongst others by the absence of a well-developed allantoic placenta and by the very helpless condition in which the fœtus is born, was once very widely distributed over the globe. Now, however, marsupials are numerous only in Australia, where they are almost the sole representatives of the mammalian class. There are a few marsupials elsewhere, as in America (opossums) and New Guinea; but there are no marsupials at the present time in Europe, most parts of Asia, or in Africa.

There is a good deal of uncertainty as to the relation of marsupials to the Eutheria (placental mammals). It was formerly assumed that a good many Mesozoic mammals, known only by their jaws, were marsupials; but some of these may have been Monotremes, and doubt is felt about a good many others, which, though they have points of resemblance to the marsupials, cannot, for the want of sufficient material, be definitely referred to that sub-class. Recently the discovery of a rudimentary placenta in the bandicoot (*Perameles*) as well as of some vestiges of a second dentition suggests the possibility that after all marsupials may be degenerate forms of placental mammals, or that the two may have had a common ancestry. The opinion held that (although marsupials in former ages were animals apparently very widely distributed) placental mammals are not descended directly from them is gaining ground.

The marsupials of America are all opossums (*Didelphidæ*), and this family is not represented in Australia. The ancestors of the marsupials of America are now regarded as a primitive form whence all other marsupials may have been derived.

The marsupials of Australia almost monopolise that country; thus Wallace says of it: "The Australian region is broadly distinguished from all the rest of the globe by the entire absence of all the orders of non-aquatic mammalia that abound in the Old World, except two: the winged bats (*Cheiroptera*) and the equally cosmopolite rodents. Of these latter, however, only one family is represented—the *Muridæ* (comprising the rats and mice)—and the Australian representatives of these are all of small or moderate size, a suggestive fact in appreciating the true character of the Australian fauna.

"In place of the Quadrumana, Carnivora, and Ungulata, which

> abound in endless variety in all the other zoological regions under equally favourable conditions, Australia possesses two new orders or sub-classes, *Marsupialia* and *Monotremata*, found nowhere else in the globe, except a single family of the former in America.
>
> "The marsupials are wonderfully developed in Australia, where they exist in the most diversified forms, adapted to different modes of life. Some are carnivorous, some herbivorous, some arboreal, others terrestrial. There are insect-eaters, root-gnawers, fruit-eaters, honey-eaters, leaf or grass-feeders.
>
> "Some resemble wolves, others marmots, weasels, squirrels, flying squirrels, dormice or jerboas.
>
> "They are classed in six distinct families, comprising about thirty genera, and subserve most of the purposes in the economy of nature fulfilled in other parts of the world by very different groups ; yet they all possess the common peculiarities of structure and habits which show that they are members of one stock, and have no real affinity with the Old World forms, which they often outwardly resemble" ("Geographical Distribution of Animals," p. 391).

This passage from A. R. Wallace has been quoted because much of it is applicable to the teeth.

In Australia, the present home of the marsupials, representative species abound ; that is to say, widely different though the animals really are, there are many genera and species which have the habits and, as it were, fill the place of such creatures as the Carnivora, Insectivora and Rodentia amongst the placental mammalia. And not only do they possess something of their habits and external configuration, but in those characteristic structures which are subservient to the creature's immediate wants the marsupial representatives closely mimic the more highly organised placental mammals. Thus the teeth of an insect-eating marsupial very closely resemble those of a true insectivore, though retaining certain eminently marsupial characters ; in the same way the dentition of the marsupial thylacine mimics that of a dog. (Compare Figs. 228 and 229.)

And although marsupial dentitions do vary very much, yet there are many transitional forms by which we are sometimes able to trace the successive modifications through which extreme divergence has been ultimately attained.

Just as we ascribe to placental mammals the formula—

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{3}{3} = 44$$

as the typical or parent dental formula, so to recent marsupials the following has generally been attributed :—

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{3}{3}\;m\,\frac{4}{4} = 44.$$

This formula was arrived at prior to the existence of any data as to the nature of the succession of teeth in the marsupials, and was, therefore, necessarily based only upon the forms of the teeth, which appeared to indicate such a classification, and it has long held the field unquestioned.

One fact at least is well established : in marsupials there is never any vertical replacement of teeth except at one point in the jaw, and this is always the same point. It is always the third cheek tooth from the front which is vertically replaced, in some instances both deciduous and replacing teeth being equally fully developed and in others reduction falling upon one or both.

But the advance of palæontology, by bringing to light extinct forms which may or may not have been actually marsupials, and the investigation of the peculiar succession found in recent marsupials and in creatures which appear to have been their ancestors, as well as in some Eutheria, throw doubt upon the correctness of this division into premolars and molars as differing from that found in placental mammals, and the difficulties thence arising have led one palæontologist, Ameghino, to go so far as to abandon the division altogether and to number the cheek teeth in one category as one to seven from front to back.

The close resemblance between the dentitions of marsupial and placental carnivorous animals was noted long ago by Gaudry, who. on the strength of this resemblance, assigned the same dental formula to the thylacine, to *Hyænodon*, and to the dog, viz., pm $\frac{4}{4}$ and m $\frac{3}{3}$. Lydekker has pointed out (6) that if we place side by side the figures of the dentitions of *Hyænodon*, *Borhyæna*,* *Thylacinus* (recent), *Prothylacinus*, and *Amphiproviverra*, it is obvious that to assign to them any fundamental difference in dental formula must be artificial. Yet here we have creodonts lying upon or near to the ancestral stem of the Carnivora, ancestral marsupials, and modern marsupials, and he seeks to find a dental formula for the recent marsupials which will fit the demonstrated peculiarities of their tooth-change and at the same time harmonise them with the extinct forms. This he does in the first place by adopting the view that the functional teeth of the marsupials (with the exception of the one replacing tooth) are homologous with the milk teeth of placental mammals, including amongst milk teeth in both the true molars which are never replaced in any mammal. On this interpretation the fourth marsupial cheek tooth (first true molar according to the usual designation) becomes the fourth milk molar, a tooth deciduous and replaced by a premolar in placental mammals, but not shed nor replaced in marsupials ; in other words, it is the homologue of the dm4 of *Sus* or *Canis*, and only remains because no pm4 is developed below it. It is pointed out by Lydekker that the tooth in this position differs little in form from the true molar behind it. This resemblance was the cause of marsupials having been considered as possessing four true molars. In his view the fourth permanent premolar in marsupials is not developed ;

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* *Borhyæna* is now regarded by many palæontologists as a highly specialised polyprotodont marsupial.—H. W. M. T.

indeed, only one permanent premolar, pm3, is developed, and he would write the functional marsupial dentition thus :—

$$\mathrm{mi}\,\frac{3}{3}\,\mathrm{mc}\,\frac{1}{1}\,\frac{\mathrm{mpm}_1\ \mathrm{mpm}_2\ \mathrm{ppm}_3\ \mathrm{mpm}_4\ \mathrm{m}_1\ \mathrm{m}^2\ \mathrm{m}_3}{\mathrm{mpm}_1\ \mathrm{mpm}_2\ \mathrm{ppm}_3\ \mathrm{mpm}_4\ \mathrm{m}_1\ \mathrm{m}_2\ \mathrm{m}_3},$$

or briefly—

$$\mathrm{i}\,\frac{3}{3}\,\mathrm{c}\,\frac{1}{1}\,\mathrm{mm}\,\frac{3}{3}+\mathrm{pm}\,\frac{1}{1}\,\mathrm{m}\,\frac{3}{3}\ \text{(cf. p. 323).}$$

But whatever explanation we adopt of the homologies of the teeth of marsupials, and of the replacing teeth in particular, some considerable difficulties remain, and the question is not as yet to be regarded as finally settled. For if the deciduous tooth and its successor are regarded as belonging to different serial dentitions, it is equally strange whether we consider the milk dentition to have been reduced to one functional tooth, the others having been suppressed so very completely (*i.e.*, if we regard it as the last trace of a disappearing milk dentition), or if we consider the single successional tooth as the sole representative of a commencing second dentition. And this anomaly was established in very early geological times, in *Triconodon* and others. It will therefore be necessary to consider the various hypotheses which have been advanced to explain the anomaly, and in the present edition the lettering of the figures and to some extent the letterpress have been left unaltered, so that they follow the older theory of there being three premolars and four true molars.

An excess over the total numbers of the typical mammalian dentition is, however, more common in marsupials than in placental mammals. [In *Macropus billardieri* Hopewell-Smith and Tims have found what they believe to be evidences of six incisors on each side in the upper jaw. In the lower jaw five ante-molar teeth are represented, but whether the most posterior is to be regarded as a canine, or as the outermost incisor, the canine having disappeared, these writers are unable to determine (3). This affords some evidence of a polyprotodont ancestry.]

M. F. Woodward (16) examined by means of serial sections, as well as by clarifying whole jaws in clove oil, a very fine series of marsupial embryos. He found that in *Petrogale* (one of the kangaroo family) there are no less than six incisors in the premaxillary bone, of which three were minute calcified vestigial teeth, while the other three were in the stage of tooth-germ only, but were of far larger size.

The opossums have ten incisors in the upper and eight in the lower jaw ; the thylacine, very dog-like in its dentition, has eight upper incisors ; whilst in the little ant-eating *Myrmecobius* the number amounts to a total of fifty-two or fifty-six teeth, having eight or nine molar and premolar teeth on each side of the jaw.

But though after careful investigation Woodward was at that time fully convinced that the teeth did not belong to two dentitions, but that they, like the rest of the functional series, certainly all belonged to the milk series, he later on partly abandoned this view ([16]).

Moreover, he holds that this animal possesses five premolars. This is less of a difficulty than it would otherwise be, as the recent *Myrmecobius* has eight or nine cheek teeth on each side, and the ancient *Amphilestes* had twelve, of which, judging by form, six would be classified as premolars.

It was first pointed out by Flower ([2]) that in recent marsupials, and in such extinct forms as were then known, there is only a successional tooth developed at one point in the jaw. Only one of the premolars (the third, or hindmost according to the old view) has vertically displaced another tooth. From this it was at first argued that the whole milk dentition consists of four milk molars (one on each side of each jaw), there being no succession among incisors nor canines in any known marsupial. This view is now partly obsolete. It was further pointed out by Flower that the extent to which the solitary displaced molar is developed varies much in the different families: no trace of any succession has been observed in the wombat; in *Thylacinus* the small deciduous molar is calcified, but is absorbed or shed prior to any other teeth being erupted; whilst in the kangaroos it is retained till a much later period (see p. 379), and in the kangaroo-rat (*Hypsiprymnus*) the deciduous molar has not yet given place to its successor at the time when the last permanent molar has come into place, so that it, for a long time, ranges with the other teeth and is functional.

This subject was further investigated by Oldfield Thomas, who found that the *Dasyuridæ* present the same deciduous dentition as the other families, that is to say, that some have a well-developed deciduous molar, and that it occurs in various phases of reduction, some having none at all ([7]). This author, writing of *Phascologale*, one of the *Dasyuridæ*, says:—

"The normal state of a member of this group is to have three well-developed premolars, the last one of which has a (milk) predecessor. Then a tooth reduction has taken place, all of which has fallen upon what is evidently a peculiarly plastic tooth, *i.e.*, pm4, and this, with the (milk) tooth preceding it, has been decreased in various degrees and in the end suppressed, as in the allied genera *Dasyurus* and *Sarcophilus*."

Those species which have a large pm4 have preceding it a tricuspid (milk) tooth, but as pm4 gets reduced the tooth preceding it is reduced still faster till it quite aborts; even then the pm4 presents the peculiarity of not being erupted, and indeed not being calcified, until later than the other teeth.

It will be observed that he speaks of the replacing tooth as the fourth premolar, as in fact homologous with the last premolar of placental mammals, although marsupials develop but three functional premolars, as then believed.

Even assuming that no living marsupial has more than three premolars, it had been presumed that four was the original number, as in placental mammals, and Oldfield Thomas had found in *Dasyurus* and in *Phascologale dorsalis* a fourth tooth, in the position of pm2; he infers, therefore, that it is pm2 which has been lost by recent marsupials, and further points out that a marked gap exists in this situation in *Didelphys*, *Perameles*, and others. If this be so, it to some extent militates against the acceptance of Lydekker's marsupial dental formula.

[Hopewell-Smith and Marett Tims have recently (*loc. cit.*) investigated the tooth-genesis in the wallaby (*Macropus billardieri*) and have confirmed Oldfield Thomas' conclusion that pm2 is the missing tooth in the premolar series of the adult marsupial dentition. This tooth is represented by a vestigial enamel-organ which is connected to the oral epithelium by a remarkably long neck. The enamel-organ is in fact crowded out of its normal position, and comes to lie deeply imbedded in the jaw (Fig. 224). This also confirms the view that the marsupials originally possessed the typical mammalian number of four premolars, and that the vertical tooth replacement is concerned with pm4.]

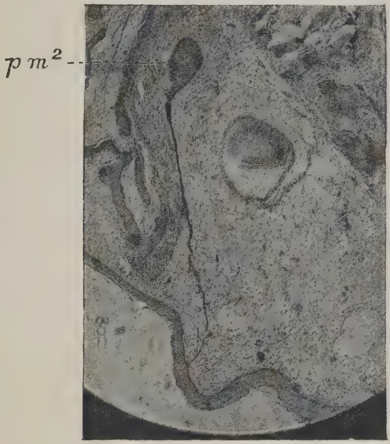

FIG. 224.—Showing the deeply situated bulbous rudiment of pm2 with the very long neck of the enamel-organ, reaching to the surface of the oral epithelium. (After Hopewell-Smith and Tims, Proc. Zool. Soc. Lond., 1911.)

In the Mesozoic *Triconodon*, which had seven cheek teeth, it was the fourth which had a vertical successor, and in Miocene formations in South America dentitions resembling the recent *Thylacinus* have been found in which there are two replacing teeth, and not merely one (*Prothylacinus*, *Borhyæna*), these being apparently premolars 2 and 3.

To recapitulate, then, we have in recent marsupials three cheek teeth which, judging them by form alone, we should be inclined to call premolars, of which the last one only is vertically replaced. Behind these come four teeth which we should, again judging by form alone, be inclined to call true molars.

But when we extend our survey to extinct forms this classification becomes less satisfactory, and to meet the difficulty Lydekker, who points out that Owen more or less anticipated him in this view, makes the following proposal. Premising that all true molars are homologically milk teeth, and that, with the exception of the one replacing tooth, all the teeth of marsupials belong to the same series, he regards their dentition as a persistent milk dentition plus one tooth of a successional dentition. He would call those milk molars of a placental mammal, which are displaced ultimately by successional teeth or permanent premolars (pp), milk premolars (mp). Hence he would write the formula of a marsupial thus :

$$\mathrm{mi}\,\frac{3}{3}\,\mathrm{mc}\,\frac{1\ \mathrm{mp}_1\ \mathrm{mp}_2\ \mathrm{pp}_3\ \mathrm{mp}_4}{1\ \mathrm{mp}_1\ \mathrm{mp}_2\ \mathrm{pp}_3\ \mathrm{mp}_4}\,\mathrm{m}\,\frac{1\,.\,2\,.\,3}{1\,.\,2\,.\,3},$$

or shortly

$$\mathrm{i}\,\frac{3}{3}\,\mathrm{c}\,\frac{1}{1}\,\mathrm{mp}+\mathrm{pp}\,\frac{4}{4}\,\mathrm{m}\,\frac{3}{3}.$$

There would then be no essential difference as to number of premolars and true molars between the marsupials and the placental mammals, and this view is adopted by Wortman.

The question whether the tooth change of the marsupials is the remnant of a more complete change in an ancestral form, or is the dawning of a more complete change, as believed by Flower, has been discussed at length by Oldfield Thomas.

That it is the first formation of a change he formerly held strongly, (i.) because the marsupials are at a lower stage of evolution than other mammals, and so it would be unlikely that they had once evolved a change, and then evolved it away again ; (ii.) because five out of the six marsupial families have precisely the same amount of tooth change, which would be unlikely if it were an atavism ; (iii.) and because no fossil marsupials then known presented any indication of a fuller change, but had just the same.

But in the face of the discoveries of Kükenthal, Röse, Leche, and others, Oldfield Thomas abandoned this position and accepted the view as incontestable that the functional dentition of marsupials is homologous with the milk dentition of true diphyodonts, there being a single permanent or successional tooth developed on each side of the jaw.

But before entering further upon this question it is desirable to clear up if possible the homologies of the whole functional set of teeth of marsupials. With regard to this the most diverse opinions still prevail.

When it was discovered by Flower that there was a vertical succession of one tooth only, the last of the then apparent premolars, he at first thought that all the rest of the functional teeth, with this one exception, corresponded to the permanent teeth of other mammals ; and that there was a milk dentition consisting of one tooth only, variable in the extent to which it was developed, so that he regarded it as presenting the first appearance of a milk dentition. There were many difficulties in the way of accepting this view, which was nevertheless accepted by Oldfield Thomas in an elaborate paper on the *Dasyuridæ* (7). But Kükenthal and Röse, investigating serial sections of the jaws of young animals, found that the dental lamina presented swellings to the lingual side of the developing functional tooth-germs, which they interpreted as being aborted permanent teeth, and hence they came to the conclusion that the whole of the functional set must be regarded as the milk teeth, and that the permanent teeth were suppressed. And this view was cordially accepted by Thomas (who abandoned his earlier ideas on the subject), and more recently by Lydekker.

The molars, originating from the dental lamina and never having had any predecessors, they regard also as belonging to the milk series, just as they regard them in other mammals.

This general idea, that the functional teeth really represent the milk dentitions of other mammals (with, perhaps, the solitary exception of the one replacing premolar), has gained somewhat general acceptance ; and it has been sought to explain the various other phenomena presently to be described in accordance with this hypothesis.

Woodward (16) in 1892 discovered that in some of the *Macropidæ* there were a number of small calcified teeth, in addition to the tooth-germs of the functional teeth. In *Petrogale* he found, in addition to the tooth-germs of the three functional incisors, three minute but calcified rudiments in the upper jaw, and two in the lower. Whilst accepting the view that the functional incisors were of the milk dentition, he regarded the rudiments which he discovered as belonging to the same series ; that is to say, he considered that they represented additional suppressed teeth, and hence were indications that the polyprotodont marsupials had six incisors on each side in the upper jaw. Subsequently, however, he adopted Leche's interpretation that they were premilk teeth.

Leche (4 and 5) described in *Myrmecobius* the occurrence of calcified rudiments which lay to the labial side of the functional tooth-germs, and therefore were referable to an antecedent set of teeth. Bound by the idea that the functional teeth are milk teeth, he was compelled to assume that these rudiments are referable to a premilk series, and this interpretation was accepted by Woodward, who discovered some additional calcified rudiments in *Myrmecobius* and held that he had found confirmation of this by the discovery of similarly placed rudiments in *Phascologale*.

It will be seen that so far the interpretation of the homologies of the functional teeth turns wholly upon the degree of significance which is attached to the observations of swellings of the tooth-band to the lingual side of the functional tooth-germs, that is to say, to the observations of Röse and Kükenthal, who interpreted them as unquestionable tooth-germs, and whose interpretation was for some time accepted almost without question.

But if these are not real tooth-germs, that is to say, if they are only swellings such as may occur in the residual tooth-band without such definite significance, the whole case falls to the ground. And this question is strongly raised by Messrs. Wilson and Hill (15), who, in an exhaustive paper upon the development of the teeth in *Perameles*, have ably summarised the whole matter (of this summary the author has made much use).

They hold that (using the criteria laid down by Leche, who, however, has not been led to this conclusion by his own criteria) there is no adequate evidence that the differentiation of these swellings is sufficient to entitle them to be considered as tooth-germs, and hence that there is no evidence that Leche's tooth rudiments in *Myrmecobius* are to be regarded as "premilk," but that there is a simpler and less far-fetched interpretation, namely, that they, as well as the germs observed by themselves, by Woodward and others, are ordinary milk teeth.

Hence their conclusion is, that the functional dentition of a marsupial is the permanent dentition of other mammals, and that the milk dentition is the one upon which suppression has fallen in varying degrees of completeness. This conclusion had also been arrived at independently by Marett Tims ([9] and [10]). The marsupials, according to these writers, are to be regarded as truly diphyodont mammals, in which the milk dentition, not wanted owing to the peculiar conditions of the birth of the young and their long sojourn in the pouch attached to the teats of the mother, has practically vanished.

This view, if adopted, greatly simplifies the whole question, and is the one to which the author inclines from a study of the various papers published upon the matter; it, of course, does away with the somewhat improbable assumption of the existence of a "premilk" dentition in the marsupials.

The observations of Röse upon the early conditions of the wombat are important in this connection; he found that there were rudiments of calcified teeth entirely unrepresented in the functional dentition, and that they belong to a generation of teeth antecedent to the functional teeth. Moreover, he finds in the place subsequently occupied by the single persistent premolar a precociously calcified tooth with a large germ to its lingual side, which latter he regards as the germ of the functional tooth.

To fit in this observation of Röse's with the widely accepted views as to the functional teeth of marsupials being the milk teeth leads into difficulties, and Röse himself frames the far-fetched hypothesis that in the wombat there is a difference in the homologies of the teeth in the front and the back of the jaw, and so that this animal stands alone in a very exceptional condition as regards its dentition. Leche, on the other hand, sets aside Röse's difficulties (arising from Röse feeling compelled to regard the calcified precocious germs of the front of the jaw as true milk teeth), and relegates the functional teeth of the wombat to the milk dentition.

The view of Wilson and Hill (*vide supra*) reopened the question of the homologies of the replacing tooth and its predecessor. They regard the deciduous tooth as a true milk tooth, ranging with the other calcified and uncalcified milk rudiments (premilk of Leche and Woodward), and point to the fact that it, like them, has in some cases completely disappeared, as in *Dasyurus*, though even in this animal it is present as a calcified vestige in the mammary fœtus, while in *Thylacinus* the successional premolar is a well-developed tooth, and is preceded by a minute and rudimentary milk tooth shed in infancy.

Hence they hold that there is a process of reduction affecting first the milk tooth, and finally both the milk tooth and its successor, as in *Dasyurus*, and that this process of reduction is the same that has affected all the other milk teeth; it is the hindmost member of the milk series, and upon it reduction has come last, and so less than upon the more anterior milk teeth.

For the curious fact that there is a succession at one point in the jaw only, Oldfield Thomas suggested as an explanation that there first took place a retardation of a back permanent tooth, perhaps useful for "packing" purposes in a jaw as yet small, and that when the retardation had gone to a certain point a milk tooth was developed to fill the gap in the series which would otherwise have existed.

A different light was thrown upon the subject by the very interesting paper of M. F. Woodward; he found that even the successional tooth-germ itself develops from the primitive tooth-band, between pm3 and pm4 as they are usually supposed to be; he therefore believes that it really belongs to precisely the same series as the others, and that it is delayed by being crowded out. This suggestion, that it really belongs to the same series as the other teeth, *i.e.*, the milk series, seems much more probable than that just one single tooth of a different series should attain to the very full development which it does in some genera.

Röse comes somewhat near to the same idea, as he urges that in some species of *Didelphys*, *Perameles*, &c., it has been shown that no tooth change takes place after the rule laid down by Flower and Thomas, but that a late tooth thrusts itself up into the row between two of the others without the absorption of any of them, so that the question arises whether there is any real tooth change in marsupials, in the ordinarily accepted sense of the word.

Leche has apparently adopted the belief that the single tooth change is the herald of a new dentition, but he holds to the idea that the functional teeth are milk teeth, and regards the epithelial swellings of Kükenthal and Röse not as remnants of a lost second set, but as heralds of a second set not yet acquired by the marsupials.

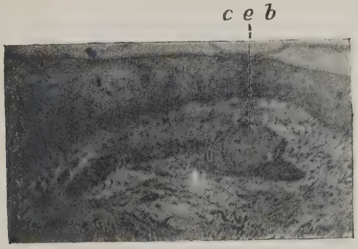

Fig. 225.—Showing a concentric epithelial (*c e b*) from the jaw of *Macropus billardieri*. (After Hopewell-Smith and Tims, Proc. Zool. Soc. Lond., 1911.)

The whole question of the single tooth replacement has been reinvestigated by Marett Tims (11). He draws attention to the significant fact that the deciduous tooth, like the posterior deciduous premolar of the dog, man, and certain insectivores, is molariform in pattern, and therefore unlike its successor; and, further, that the successional tooth develops in all these cases *in front of* its predecessor, the reverse of that which obtains in all other instances of tooth replacement. He therefore regards, as Woodward had done, all the teeth of the marsupials as belonging to the same series, but differs from the latter writer in regarding this series as the homologue of the successional series of the Eutheria (*vide supra*). According to this interpretation the deciduous tooth in all the animals above mentioned is in reality the first of the molar series pushed over the top of the replacing tooth, which is the last of the premolar series, due to a progressive shortening of the jaw. The degree to which this shortening has taken place determines the age at which the tooth succession occurs. In *Myrmecobius*, with its very elongated narrow jaws, no tooth change is definitely known to occur, and this animal possesses a larger number of molar teeth than any other mammal, a further evidence of its primitive character. In confirmation of this interpretation Tims believes that he has found in the dog a vestige of the true dpm^4, crowded between the ppm^4 and its predecessor (?m^1). With regard to the molar teeth, he agrees with

M. F. Woodward, Lataste, and Magitot in regarding them as belonging to the successional series, the vestiges of their predecessors being still preserved as "concentric epithelial bodies."

That such a projection of the anterior molar teeth over the top of the posterior premolars does take place, and, moreover, that it is a phenomenon of considerable antiquity, is evidenced by the accompanying Fig. 226.

The question is, however, far too lengthy for full discussion in these pages. For further information upon it the reader is referred to Messrs. Wilson and Hill's able summary, to Leche, and to the papers of Kükenthal, Röse, Woodward, Thomas, and Marett Tims.

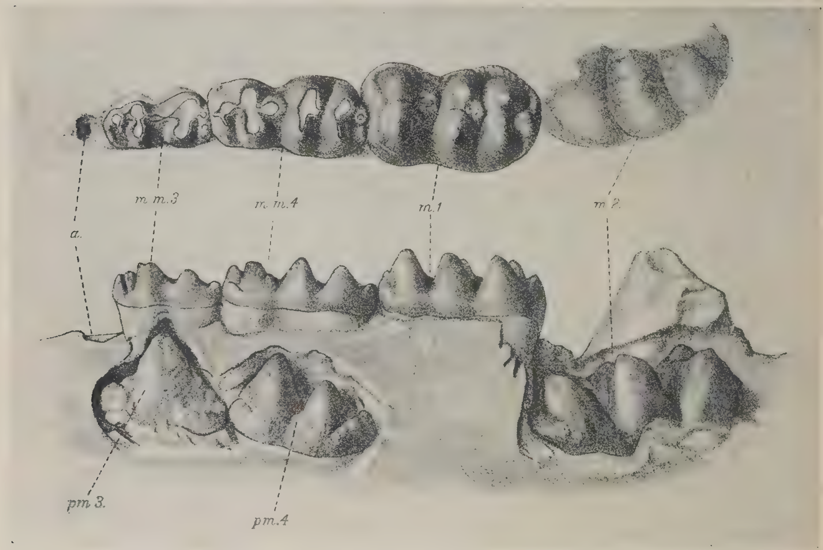

Fig. 226.—Mandible of a young individual of *Palæmastodon wintoni*, showing the crown view of the right milk molars and a side view of the cheek teeth of the right side, the pm3 and pm4 replacing mm3 and mm4. The first true molar (m1) and the germ of the second (m2) are also seen. (After C. W. Andrews, Phil. Trans. Roy. Soc. Lond., vol. cxcix., series B, 1908.)

A further peculiarity of the marsupials is the structure of their enamel, which is penetrated by the dentinal tubes. Sir John Tomes, some years ago (12), described and figured the teeth of a large number of marsupial genera, and found that, although in the different families the tube system of the enamel varied in its richness and in the depth to which the tubes penetrated, yet it was conspicuously present in the whole class, with the sole exception of the wombats, in which nothing of the kind is to be found. The dilatation noticeable at the boundary line of the enamel and the dentine (see Fig. 227) is a kind of clumsy joint brought about by the coalescence at this point of the tube-forming cells, on the one side odontoblasts, on the other enamel cells.

The dilatation is not universally present, but a well-marked curve at the juncture of the enamel and the dentine sometimes occurs, as well as various curves in the course of the tubes through the enamel.

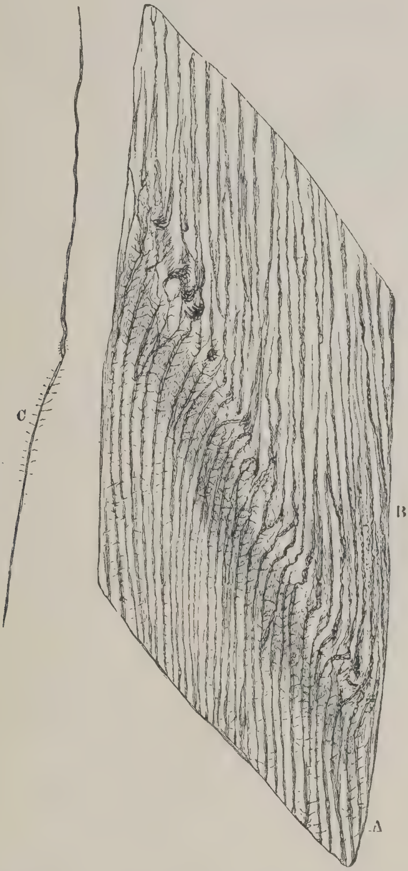

FIG. 227.—Enamel and dentine of a kangaroo (*Macropus major*).

The dentinal tubes in the dentine (A) are furnished with numerous short branches at the line of juncture with the enamel; they are dilated and a little bent out of their course, while beyond the dilatation they pass on through about two-thirds of the thickness of the enamel in a straight course and without branches. Only a part of the whole thickness of the enamel is shown in the figure. B. Enamel penetrated by the tubes. C. Individual dentinal tube.

The extent to which the tube system exists in the enamel varies much in different families. It attains its utmost development in the *Macropodidæ,* and is more feebly present in some *Dasyuridæ*, whilst in *Myrmecobius*, and yet further in *Tarsipes*, it is reduced to small limits.

[The pattern of the enamel and its penetration by tubes has recently assumed an added importance from the recent researches of Thornton Carter, from which it would appear that the pattern of the enamel in recent marsupials is by no means always as simple as had previously been supposed (*e.g.*, *Dasyurus*, *Macropus ruficollis*). Furthermore, that the tubular penetration of the enamel takes place in the Sparassodont genera *Cladosictis* and *Pharsophorus* as well as in the Creodont *Hyænodon.* Carter concludes from these facts that the two Sparassodont genera are thus brought into even closer relationship with the recent carnivorous marsupials, and that this tubular penetration of the enamel in *Hyænodon* is " additional evidence in favour of the common origin of the marsupials and the earlier Monodelphia " (1).]

It is said by von Ebner that the tubes in marsupial enamel are not in the axes of the prisms, but run between them, but this is a point upon which it is a little difficult to be certain ; and the author is of opinion that the tubes are in the substance of the prisms. (See p. 59.)

[Carter (*loc. cit.*) agrees with Leon Williams, who states that the majority of the tubes appear to be definitely in the substance of the rods, while a minority appear to be between them.]

Recent marsupials are grouped into—

Polyprotodonts.—Incisors numerous, small, and subequal ; canines pronounced and strongly tuberculated, molars in many sharp-cusped, *e.g.*, *Didelphys.*

Diprotodonts.—Incisors not more than $\frac{3}{3}$, often $\frac{3}{1}$ and sometimes as low as $\frac{1}{1}$. The first upper and the lower incisors are large, with cutting edges.

Upper canines absent or small, lower absent. Molars bluntly tuberculated or ridged, *e.g.*, kangaroo. Under the diprotodont division come the wombats, which have all their teeth with persistent pulps, and their incisors, rodent-like, with enamel on their front surfaces only.

Among the polyprotodont series there exists one genus of flesh-eating marsupials whose ferocity is such as to have gained for them the names of wolf and tiger, while the resemblance of the head to that of a dog has given origin to the popular name of " dog-headed opossums." *

The resemblance to the dog in dentition is even more close than in external form ; whilst retaining certain marsupial attributes, the teeth of the thylacine are, so far as their working capabilities go, almost exactly like those of the dog. The dental formula is—

$$i\,\frac{4}{3}\;c\,\frac{1}{1},\ \text{cheek teeth}\ \frac{7}{7}.$$

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* It has, of course, no real relationship to the true opossums, which are not found in Australia.

The incisors are small, close set, and sharp-edged, the outermost being somewhat caniniform. The canines are stout, pointed teeth, not quite so long relatively as those of a dog. The premolars are conical, implanted by two roots, and very similar to those of the dog; they are followed in the upper jaw by four (?) molars, which increase in size from the first to the third, but the last true molar is again a smaller tooth.

Fig. 228.

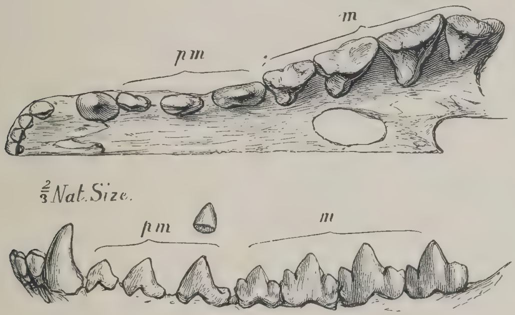

Fig. 229.

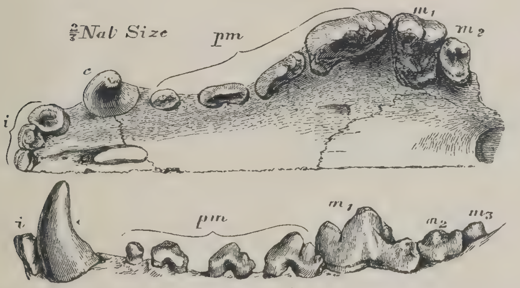

Fig. 228.—Upper and lower teeth of the thylacine. The rudimentary milk molar, which is absorbed before birth, has been placed over the third or last of the premolars, which succeeds to it vertically. Pending agreement amongst naturalists as to the homologies of the premolars and molars, the old lettering has been left upon this and the ensuing figures.

Fig. 229.—Upper and lower teeth of a dog, which are placed side by side with those of the thylacine, to show the many points of resemblance between the two dentitions.

The upper molars are all of the "carnassial" pattern; there is a "blade" elevated into subsidiary cusps, and internally to this a "tubercle," supported by a thin root.

The lower molars also bear some resemblance to the carnassial teeth of the dog, consisting of a strong, sharp-edged blade, with anterior and posterior subsidiary cusps, the latter being somewhat broad and tubercular.

An allied animal (*Dasyurus ursinus*), though smaller than the thylacine, and having teeth of a less sectorial character, is so destructive to sheep and so fierce and untamable that it has earned the name of "Tasmanian Devil."

Within the limits of the same genus a species (*Dasyurus viverrinus*) is to be found in which the molar teeth are studded over with long sharp cusps, like the teeth of Insectivora, a group which it resembles both in its habits and food.

A number of smaller marsupials approximate in their dentition more or less to the insectivorous type, whilst a tolerably complete chain of existing forms serves to bridge over the gap between the rapacious *Dasyuridæ* and the herbivorous kangaroos and wombats.

Amongst the opossums the larger species have large canines, and the dentition in its general features approximates to the *Dasyuridæ;* they feed upon birds and small mammals, as well as upon reptiles and insects, though the smaller species are more purely insectivorous.

Myrmecobius, a small Australian marsupial of insectivorous habits and dentition, is remarkable as having teeth in excess of the number of the typical mammalian dentition,* having—

$$\mathrm{i}\,\frac{4}{3}\ \mathrm{c}\,\frac{1}{1},\ \text{cheek teeth}\ \frac{9}{9},$$

though of course there is a doubt as to their division into premolars and molars.

It is further remarkable in that its milk (or premilk ?) rudiments are carried further than those of most other marsupials. Leche described calcified predecessors to $\mathrm{i}\,\frac{1}{-}$, $\mathrm{i}\,\frac{2}{-}$, and to $\mathrm{i}\frac{-}{2}\,\frac{-}{\mathrm{c}}$, and an uncalcified predecessor to $\frac{-}{\mathrm{i}3}$, and to these Woodward added $\frac{\mathrm{i}3}{-}$, $\frac{\mathrm{i}4}{-}$, and $\frac{\mathrm{c}}{-}$; in the lower jaw he found the same as Leche, and also well-differentiated germs of $\frac{\mathrm{dpm}\ 4}{\mathrm{dpm}\ 4}$, so that its full milk (or premilk ?) formula was—

$$\mathrm{i}\,\frac{1234}{23}\ \mathrm{c}\,\frac{1}{1}\ \frac{\mathrm{dpm}\ 4}{\mathrm{dpm}\ 4}.$$

In the phalangers, nocturnal arboreal animals found in Australia and a part of the Malay Archipelago, the canines, though present, are feeble; an interspace also separates the incisors from the molar series.

The lower incisors, reduced to a single pair, are procumbent and grow from persistent pulps. There is thus, functionally, some faint approach to the character of a rodent dentition, as may be seen by an inspection of the accompanying figure, though there is a strongly marked transverse condyle to the lower jaw. *Phascolarctos cinereus* has been shown by Oldfield Thomas to have the same reduced deciduous tooth as *Thylacinus*.

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* A possible explanation of the large number of molar teeth has been suggested on a previous page (p. 369).

The very sharp cusps of the molars, in the lower jaw somewhat concave on their inner aspect, are so formed as to long preserve their sharpness and accurate coadaptation.

The name "**Kangaroo Rats**" (*Hypsiprymnus*) is applied to a genus consisting of about a dozen species; they are all small creatures, not much larger than rabbits, but having the general proportions of kangaroos. They are quiet, gentle little creatures, of strictly herbivorous habits, and they are interesting to the odontologist as possessing a dentition which throws some light upon several anomalous extinct forms whose habits and affinities have been the subject of much controversy.

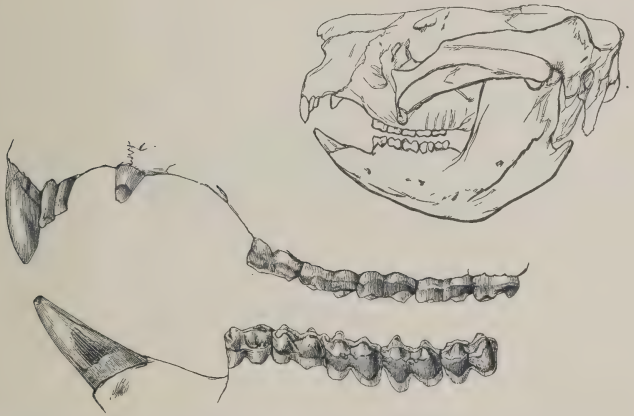

FIG. 230.—Teeth of *Phascolarctos cinereus*. An outline figure of the skull is placed above to show the general "rodent" aspect of the skull.

The dental formula is—

$$i\,\frac{3}{1}\;c\,\frac{1}{0},\ \text{cheek teeth}\ \frac{5}{5}.$$

The first pair of upper incisors are sharply pointed, are directed nearly vertically downwards, and grow from persistent pulps. The second and third do not grow from persistent pulps, and their worn crowns do not attain to the same level as those of the first pair.

All three pairs are antagonised by the single pair of large procumbent lower incisors, of which the sharp points meet the first pair of upper incisors, while the obliquely worn surfaces behind the cutting edges impinge against the second and third upper incisors.

The arrangement of the incisors and the sharpness of their cutting edges are calculated to effect the same objects as those attained by the incisors of a rodent. A still closer resemblance would be brought about by the dwindling (which occurs in other genera) and final disappearance of the second and third upper incisors, and a compensating extra development of the first pair.

The canines are not large, yet they are not so small as to be termed rudimentary ; in the lower jaw they are absent.

Only one premolar exists in the adult, and this is a very peculiar tooth ; its crown is very long from back to front (at least twice as long as any of the molars, and in some species as long as three of the molars), and consists of a finely furrowed blade with a sharp edge ; the blades of the upper and lower teeth slide over one another. Behind this there are four (?) true molars, with square quadricuspid crowns, which become much worn down by use.

The last and only (?) premolar, the tooth to which attention has already been drawn on account of its size and other peculiarities, by virtue of its great size displaces not only the usually deciduous molar, to which it is the legitimate successor, but also turns out the premolar in front of it.*

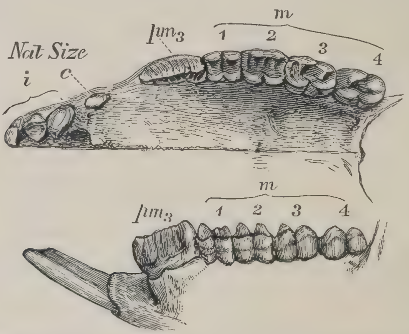

Fig. 231.—Upper and lower teeth of *Hypsiprymnus* (*Bettongia*) (graii ?). The detention represented is that of the adult animal, the permanent premolar being already in place.

In this particular the succession of the teeth in the *Hypsiprymnus* is the same as that of the true kangaroo, which may be understood by a reference to Fig. 232.

There are some extinct animals, perhaps marsupials, known only by their jaws, which have been the subject of much controversy. Professor Owen, basing his arguments largely upon the presence of premolars which possessed elongated and sharp-edged blades, held that *Plagiaulax* (cf. p. 343) and *Thylacoleo* were carnivorous, saying of the latter that it possessed the simplest and most effective dental machinery for predatory life known among mammalia. Dr. Falconer in the case of the former, and Sir William Flower in the case of the *Thylacoleo*, have shown this view to be untenable, or at least unsupported by adequate evidence.

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* The old nomenclature has been here retained. If Lydekker's view be accepted, these teeth would be two premolars and only three true molars.

A clue to the nature of the great blade-shaped teeth of these extinct creatures is afforded by the form of the premolar of the herbivorous *Hypsiprymnus* (see Fig. 231). The incisors are reduced in number, and are large; the teeth between them and the large premolar are stunted; but both these points are true of the herbivorous kangaroos. The *Thylacoleo* differs, however, from all known animals by the immense size of the thin-edged premolar (worn flat in aged animals), and by the rudimentary condition of its true molars. But its incisors, lying forwards and closely approximated in the middle line, are particularly unsuitable for catching and holding anything alive and struggling, whilst the nearest resemblance to its blade-shaped tooth is to be found in harmless herbivorous creatures, so that the balance of evidence is much against Professor Owen's view.

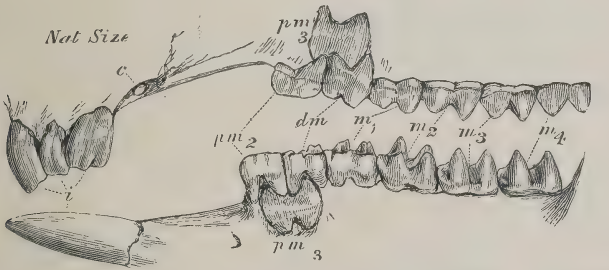

FIG. 232.—Upper and lower teeth of *Halmaturus ualabatus*. The successional premolar is not yet erupted, and is shown in its crypt; when it comes into its place it will displace the deciduous molar, and one of the anterior premolars as well. In the upper jaw a rudimentary canine is shown. The point of the lower incisor would fit, in closure of the mouth, behind the long anterior upper incisor, but the width of the figure does not admit of the teeth being placed in their true relative positions without reduction in size.

The dental formula of *Thylacoleo* was—

$$\frac{3}{1}\ \mathrm{c}\ \frac{1}{0}\ \mathrm{p}\ \frac{3}{1}\ \mathrm{m}\ \frac{1}{2}\ \left(\text{cheek teeth } \frac{4}{3}\right).$$

The first upper incisor was very large, and the second and third very small, as were the canine and the first two upper premolars; but the last upper and the only lower premolars * were great blade-shaped teeth like the large premolars of *Hypsiprymnus*, but considerably larger. Thus its useful teeth were only a pair of incisors above and below and a pair of sectorial premolars.

The **Kangaroos,** comprising many species of very varying size, are (with the exception of a few old males) all docile creatures of herbivorous habits, recalling in some particulars the ruminants.

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* Lydekker suggests that there were other lower premolars present, but they were soon lost.

Their dental formula is—

$$i\,\frac{3}{1}\;c\,\frac{0}{0},\text{ cheek teeth }\frac{5}{5}.$$

The three pairs of upper incisors are more equal in size than in the *Hypsiprymnus*, and the central pair do not grow from persistent pulps. The lower incisors are very peculiar teeth: they are procumbent, projecting forwards almost horizontally, and are much flattened from side to side, their outer surfaces being but slightly convex, and their inner surfaces flat, with a median ridge. Their margins are almost sharp. There is an unusual amount of mobility between the two halves of the lower jaw, so that these two teeth can be to a slight extent separated from one another.

The upper canine is often present as a very minute rudiment, but in no kangaroo does it attain to a greater size.

The dentition of the kangaroo is somewhat perplexing to the student, for two reasons: the one that the premolar not only displaces the solitary deciduous molar, as in *Hypsiprymnus*, on account of its greater size, but also the next premolar which was situated in front of the deciduous molar; and, moreover, in animals past adult age, teeth are shed off from the front of the molar series till at last only the last two true molars on each side remain.

The dentition of the kangaroo at successive ages may be thus represented:

$$i\,\frac{3}{1}\;c\,\frac{0}{0},\text{ cheek teeth }\frac{6}{6},\text{ of which one is deciduous,}$$

or, in all, six molar teeth. Then the third premolar displaces the second premolar as well as the usually deciduous molar, giving—

$$\frac{3}{1}\;c\,\frac{0}{0},\text{ cheek teeth }\frac{5}{5},\text{ of which one is the successional tooth, or,}$$

in all, only five molar teeth.

Then, one after another, teeth are shed off from the front of the molar series, just as in the *Phacochœrus* (see p. 457), till all that is left is—

$$i\,\frac{3}{1}\;c\,\frac{0}{0}\;p\,\frac{0}{0}\;m\,\frac{2}{2}.$$

The deciduous molar of the kangaroo is a fully developed tooth, which takes its place with the other teeth, and is not distinguished from them by any special characters, so that mere inspection of the jaw of a young kangaroo having it in place, at the same time with a premolar in front of it and four true molars behind it, would not lead an observer to suspect its true nature.

No existing creature serves to connect the kangaroo closely with the wombat, but the extinct *Diprotodon* appears to have in a measure bridged across the gap.

The **Wombats** (*Phascolomys*) are heavily built, inoffensive creatures, which burrow in the ground and subsist largely upon roots. In their dentition they closely simulate the rodents, as they possess but a single pair of chisel-edged incisors in either jaw, growing from persistent pulps, and imbedded in very deep and curved sockets. These differ from the corresponding *dentes scalparii* of true rodents in that there is a complete investment of cementum which passes over the enamel in front of the tooth as well as covering its back and sides. They are unlike the teeth of other marsupials in their structure, as the dentinal tubes do not penetrate the enamel, which is therefore probably harder and denser and so less readily worn away.

The molar teeth also grow from persistent pulps and are very deeply grooved upon their sides, so that their grinding surfaces are uneven.

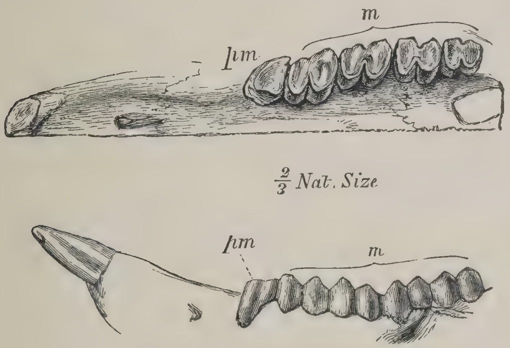

FIG. 233.—Upper and lower teeth of a wombat (*Phascolomys wombat*).

The dental formula is—

$$i\,\frac{1}{1}\;c\,\frac{0}{0},\;\text{cheek teeth}\;\frac{5}{5}.$$

The first tooth of the molar series forms a single column, whereas the deep grooving of the other teeth divides each of them into two columns. The simpler appearance, as well as analogy, would indicate that the first tooth is a premolar.

The adaptive resemblance to the dentition of the true rodents is exceedingly close, though the wombat is an undoubted marsupial; and the very closeness of the imitation is an exemplification of the fact that adaptive characters are very apt to mislead, if used for the purposes of classification.

Another peculiarity of the wombats has been described by Röse, who confirms a long-discredited statement of Owen's that deciduous teeth are found in these animals, and he further states that the wombat has two dentitions, altogether like a placental mammal.

Röse finds that there are calcified predecessors to the functional incisors, a deciduous canine which has no successor, and deciduous premolar; all of these appear to be absorbed or shed at a very early period.

Extinct wombats, of very much larger size than the recent species, are found in the later tertiary deposits of Australia.

Amongst the marsupials there is a pretty little arboreal creature (*Tarsipes*), not larger than a small rat, which subsists upon insects and the nectar of flowers, which it reaches by means of a long protrusible tongue. Its molar teeth are rudimentary, variable in number, and are soon shed. The lower incisors, which are procumbent, are, however, retained, as are also a few small teeth which are opposed to them above.

Another remarkable South American marsupial was described by R. F. Tomes (1863) under the name of *Hyracodon*, but, this name being already appropriated, it is now termed *Cœnolestes* (Thomas) (8). Its dentinal formula is—

$$\mathrm{i}\,\frac{4}{3}\;\mathrm{c}\,\frac{1}{1},\ \text{cheek teeth}\ \frac{7}{7}.$$

It is remarkable that, though a true marsupial, it differs widely from the other American marsupials, and resembles those of Australia; the Diprotodontia have a syndactyle foot (*i.e.*, two toes contained in one skin), while among Polyprotodontia the *Peramelidœ* have the syndactyle foot, but are not diprotodonts; and American opossums are neither diprotodonts nor have they the syndactyle foot.

Cœnolestes, however, has much of the diprotodont character in its dentition, and yet has not the syndactyle foot, so that it crosses the usual lines of classification and blends the characters of several groups.

Its upper incisors are not unlike those of *Didelphys*, and it has a well-developed canine, but the front pair of lower incisors are much elongated, as in diprotodonts.

The premolars are compressed cutting teeth, the last being much the largest. The upper molars are low-crowned and nearly square in shape, the first two teeth having four cusps, the third three, and the last being a minute triangular tooth.

In the lower jaw, behind the big procumbent incisor, four minute teeth are situated; probably two are to be regarded as incisors, a canine, and one premolar; the other two premolars are narrow sharp teeth, and the lower molars are elongated from before backwards, and more or less ovate in general form.

Within the last few years Mr. Ed. Stirling has discovered a marsupial mole, to which the name *Notoryctes* has been given. By Mr. Stirling's kindness, the author has had the opportunity of examining the structure of its teeth, and has found (13) that it presents the usual marsupial character of penetration of the enamel by tubes continuous with those of the dentine, the pattern being like that of *Didelphyidœ*. Its teeth, at first pointed like those of an insectivorous animal, become worn down, probably by the sand in which it lives, and which it takes in with its food, so that they present areas of dentine surrounded by an upstanding ring of enamel, more or less elevated in places. The feeble implantation of the teeth, however, points to the food not being really hard, and the animal appears to live upon larvæ.

The wonderful diversity of the forms into which the marsupials have branched out in Australia seems to prove that they have been established in that region, and have been without the competition of more highly organised placental mammals, for a prodigious length of time; and one cannot better conclude the very brief survey of the teeth than by calling the reader's attention again to the character of the marsupial fauna—this microcosm in which every place is filled by a marsupial which mimics the placental mammal which it represents—for nowhere can we more plainly see the workings of natural selection than in areas thus isolated and deprived of immigrant creatures for countless ages.

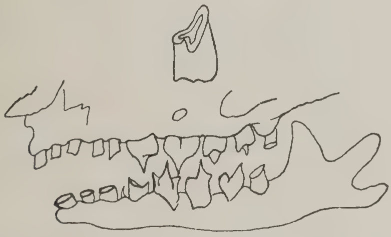

Fig. 234.—Upper and lower teeth of *Notoryctes*. The worn surface of a lower molar is shown yet more magnified in the single tooth placed above.

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CHAPTER XVI.

THE TEETH OF EUTHERIA—INSECTIVORA, GALEOPITHECIDÆ, CHEIROPTERA, CARNIVORA.

There is great difficulty in arranging placental mammals in any definite order of sequence, inasmuch as those now existing and the known fossil forms are but a small fraction of those which have once existed. And although no modern naturalist can well doubt that all existing mammals are lineal descendants of a smaller number of forms previously existing, yet they do not admit of being arranged on any one stem, and are not all lineal descendants of one another.

The mixed and uncertain affinities of some groups render any simple linear classification unsatisfactory, but two other methods may be attempted: the "circular," in which animals are grouped round generalised types; and what may be termed the phylogenetic, in which animals are, as far as possible, arranged according to their descent, in which case there would be a branching parent stem, the branches subdividing again and again.

If the lines of mammalian descent were really known, the latter is, of course, the more logical, but as no two authorities quite agree, it is for the present only partially practicable.

Dr. Wortman writes: "We know, for example, that the Primates could not be the ancestral group, for the obvious reason that they do not extend beyond Miocene time; nor the Carnivora, which appeared about the same time; nor the Rodentia, which date from the Middle Eocene; nor the Cheiroptera, which can be traced back no further than the Upper Eocene. We are, therefore, restricted in our choice to the Insectivores, Lemuroids, Creodonts, or Tillodonts, which alone of the entire series continue backwards to the base of the Eocene period. With reference to the Creodonts, I do not believe that any important distinctions exist between them and the Insectivores, while the line between this latter group and the Lemuroids and the Tillodonts becomes exceedingly shadowy at this point."

That the Insectivora are a very ancient and generalised group all naturalists agree, and the Lemuroids also go very far back.

Though questions of classification are foreign to the subject of this work, yet, inasmuch as the teeth are a very important criterion of affinity, it is desirable, but exceedingly difficult, to arrange an account of the dentitions in anything approaching to a logical sequence.

The sequence and classification of the Metatheria and of the Eutherian sub-classes, &c., adopted in the present edition of this work, are based upon, though they do not strictly follow, that given in Professor Max Weber's "Die Säugetiere" as being one of the most recent and comprehensive works on the subject.

The Teeth of Insectivora.

- INSECTIVORA
  - Menotyphla
    - *Tupaiidæ.*
    - *Macroscelidæ*, Elephant shrews.
  - Lipotyphla
    - *Talpidæ*, Moles.
    - *Soricidæ*, Shrews.
    - *Erinaceidæ*, Hedgehogs.
    - *Potamogalidæ.*
    - *Centetidæ.*
    - *Chrysochloridæ*, Golden moles.

The Insectivora form a somewhat heterogeneous order of mammals, and embrace very various forms. All of them are of rather small size, and some are very small indeed. Their diet consists for the most part of insects, and their teeth are generally adapted for this by being furnished with many pointed cusps. The best known animals in the order are the hedgehogs, the shrews, the moles, and the *Macroscelidæ* (elephant-mice). Insectivora are more abundant in Africa, Asia, and South America than in Europe. The shrews approximate in some measure towards the rodents, and the *Tupaia* is very lemurine in its characters.

They all have small, rather smooth brains and long faces. The Insectivora are ancient and in many respects generalised mammals, so that they may be supposed not to have diverged so far from the parent forms as other mammalia.

In recent Insectivora the canines are often not sharply differentiated from the incisors, and sometimes a tooth clearly of the premolar group is differentiated to function as a canine, but as this does not occur in the earlier Insectivora, it is evidently a feature subsequently acquired.

Hence it happens that different writers give different dental formulæ to the Insectivora, the differences mainly turning upon whether a tooth is regarded as a canine or not. (Cf. p. 308.) But, as pointed out by Leche and Marsh, in the oldest known mammals this tooth was always two-rooted, and the reduction to a single root is to some extent correlated with the caniniform specialisation of its crown. Thus when it has but one root this is a character acquired, and not an original distinction.

The extent to which a milk dentition is developed varies much; in many of the group it is erupted and lost early, and is more or less suppressed; whilst in others, *e.g.*, *Centetes*, *Hemicentetes*, *Macroscelis*, and *Tupaia*, it is well developed and functional for some time.

The common **Hedgehog** (*Erinaceus*) has the following dental formula :—

$$\mathrm{i}\,\frac{1\,2\,3}{0\,2\,3}\;\mathrm{c}\,\frac{1}{1}\;\mathrm{p}\,\frac{0\,2\,3\,4}{0\,2\,0\,4}\left(\mathrm{or}\;\mathrm{p}\,\frac{1\,2\,0\,4}{1\,0\,0\,4}\right)\;\mathrm{m}\,\frac{1\,2\,3}{1\,2\,3}\;\text{(Woodward).}$$

Leche, after an examination of 103 specimens belonging to seventeen species, gives us a formula common to the genus :—

$$\mathrm{i}\,\frac{1.2.3}{0.2.3}\;\mathrm{c}\,\frac{1}{1}\;\mathrm{p}\,\frac{2\,3\,4}{0\,3\,4}\;\mathrm{m}\,\frac{1.2.3}{1.2.3}.$$

But a good many dental formulæ have been assigned to it in consequence of certain difficulties and obscurities in the identification of the teeth, which have only lately been cleared up.

The differences chiefly arise because the canines are not markedly caniniform ; they are implanted by two roots, and they appear to be some little way behind the intermaxillary suture.

But it has been found that they are preceded by single-rooted caniniform teeth, and that the distance from the suture is apparent and not real, owing to the maxilla growing forward and embracing the premaxilla both on its labial and palatal aspects. In a young specimen in the possession of the author, prior to this overlapping of the maxilla the canine is seen to be close to the suture.

In the upper jaw there is a rather wide interval between the first pair of incisors, which are much the largest, lean inwards towards one another, and are somewhat caniniform in shape. The second pair of incisors are much smaller, whilst the third are intermediate in size and caniniform. The canine, though it has an indication of division into two roots, is neither a very large nor important tooth.

Leche (8) figures this tooth from four specimens of *E. europæus* showing that it varies in the same species between a tooth in all respects like a premolar and a powerful, though still two-rooted, canine. It is followed by two small single-rooted premolars, of which the second is variable and sometimes absent, and then by a large (fourth) upper premolar.

The fourth upper premolar is totally different in size and form from the third : its crown is large, squarish, and furnished with four cusps, of which the antero-external one is far the longest and sharpest.

The first upper true molar has a square crown, upon which are four sharp cusps, and in an unworn tooth a fifth small central cusp ; it is implanted by four roots. The second true molar is also square, quadricuspid, and has four roots ; but it is much smaller than the first, while the third upper true molar is quite a small, compressed, double-rooted tooth, with a thin-edged crown.

In the lower jaw the first incisors, really the second of the typical mammalian dentition, less widely separated than the upper, are also the largest ; then follows another tooth termed incisor, on account of its relation to the upper incisors when the mouth is closed. The third tooth is much larger and of peculiar form, and is the canine according to recent writers. The fourth tooth from the front is a small single tooth, like the third, but upon a smaller scale. Next behind it comes a tooth which is very much larger, and its crown carries two principal cusps with a small subsidiary cusp; this is certainly a true premolar. The next tooth (first true molar) has an oblong crown beset with five sharp cusps, of which four are arranged at the corners of a square, while the fifth, perhaps an elevation of the cingulum, lies a little in front and towards the inside of the tooth. In the second true molar the fifth cusp is but little indicated, while the last true molar is a dwarfed tooth with but one cusp.

The teeth of the hedgehog fairly represent some of the features of insectivorous dentitions, for the forcep-like incisors, the stunted or non-developed canines, and the molars bristling with pointed cusps are common to very many of the order.

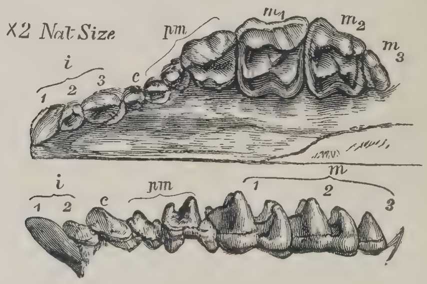

Fig. 235.—Upper and lower teeth of the hedgehog.

In the upper quinquecuspidate molars, the two outer cusps are the paracone and metacone, the two inner the protocone and hypocone, and there is a small central metaconule. Of these the order of development was—

Paracone }
Metacone } Trigon.
Protocone }
Hypocone.
Metaconule.

In the lower molars the five cusps are those of the trigon with two extra cusps, the internal entoconid and external hypoconid. Owing to the partial suppression of the paraconid, and the protoconid and metaconid being joined by a ridge, as are the entoconid and hypoconid, the resultant tooth is almost square with two transverse ridges. The order of appearance of the cusps is—

Protoconid.
Metaconid.
Entoconid.
Hypoconid.
Paraconid.

Thus in their order of appearance the cusps of the upper teeth do fit in with what might have been expected on the tritubercular theory.

In a former edition of this book the persistent dentition of the hedgehog was stated to be a mixture of replacing teeth with persistent milk teeth. This view, which was given on the authority of Leche, has been proved by that observer and by Woodward to be incorrect, and it has been found that all of the teeth which persist have been preceded by tooth vestiges in various degrees of reduction.

Some of the milk teeth are well developed and functional, others, notably the upper canine, very variable in the extent to which they are developed, whilst others again are functionless and never cut the gum, but are represented by tooth-germs which undergo development only to the extent of a trifling irregular calcification.

The formula of the milk dentition may be written thus, the teeth which are functionless being printed in italics :—

$$\mathrm{di}\ \frac{1\ 2\ \mathit{3}}{\mathit{1\ 2\ 3}}\ \mathrm{dc}\ \frac{1}{\mathit{1}}\ \mathrm{dp}\ \frac{\mathit{0\ 2}\ 3\ 4}{\mathit{0\ 2}\ 3\ 4}\ \left(\mathrm{or\ dp}\ \frac{\mathit{1}\ 2\ \mathit{3}\ 4}{\mathit{1\ 0\ 3}\ 4}\right).$$

The deciduous upper canine has been found to vary between that of a minute irregular calcification (Woodward, Leche) and a fully functional tooth.

In the molar region there are to be found both a lingual continuation of the dental lamina and a slight, but constant, outgrowth on the labial side of the neck of the enamel-organ of the functional tooth (Woodward), not distinguishable from those incisor germs which are slightly calcified. He therefore concludes that there are evidences of a vestigial set, of a functional set, and of a lamina capable of going on to form an additional set in the molar region.

Gymnura, an animal of the Malay region, closely allied to the hedgehog, but in appearance more like a very big shrew, with a body a foot in length, is somewhat peculiar in possessing the whole typical number of teeth, its dental formula being

$$\mathrm{i}\ \frac{1\ 2\ 3}{1\ 2\ 3}\ \mathrm{c}\ \frac{1}{1}\ \mathrm{p}\ \frac{1\ ?\ 2\ 3\ 4}{1\ ?\ 2\ 3\ 4}\ \mathrm{m}\ \frac{1\ 2\ 3}{1\ 2\ 3}.$$

The teeth closely resemble those of the hedgehog, as in it the upper canine is two-rooted, though preceded by a single-rooted deciduous tooth. Knowledge of its milk dentition is owing to Thomas (14) and to Woodward (19) :—

$$\mathrm{di}\ \frac{1\ 2\ \mathit{3}}{1\ 2\ 3}\ \mathrm{dc}\ \frac{1}{1}\ \mathrm{dpm}\ \frac{1\ \mathit{2}\ 3\ 4}{1\ \mathit{2}\ 3\ 4}.$$

Thus, although it has four premolars retained in its functional dentition, there is a doubt whether p $\frac{1}{1}$ are not retained milk teeth. As in so many other mammals, no vertical replacement of this tooth is known : and, according to Woodward, the relation of the germ of this tooth to the dental lamina is such as to suggest that it is a milk tooth, with the lamina continued beyond it so as to have a potential source for a successor. Woodward, however, remarks that there may possibly be a later development of a successor, as the pm $\frac{1}{1}$ of the adult seems rather a stouter tooth than that of the young animal.

The second milk premolars are vestigial, and their successors prematurely developed ; the third and fourth premolars are strongly developed. There is thus a fairly complete functional milk dentition, viz., $\frac{\mathrm{di}_3}{}$ and $\frac{\mathrm{dpm}_2}{\mathrm{dpm}_2}$ only being vestigial.*

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* For a possible explanation of certain peculiarities in the tooth succession in the posterior premolar region, the reader is referred to a previous chapter dealing with the same subject in the Marsupialia.

Centetes has typical canines like a carnivore. *Hemicentetes* has canines which in no respect differ from the premolars behind it, and *Ericulus* has a sharp, long, two-rooted upper canine, in pattern of crown, an enlarged edition of the premolars behind it. There is no caniniform tooth in the lower jaw.

The **Shrews** have numerous sharply pointed teeth, the points interdigitating and fitting very closely together when the jaws are closed. There is no tooth, either in the upper or lower jaw, which is so elongated as to deserve the name of canine ; but between the incisors and the true molars are several small teeth which, by analogy, are called premolars. The true molars are not very different in pattern from those of the mole (B in Fig. 238), and present the W contour so common in the molars of Insectivora.

The most marked peculiarity in the dentition of the shrews lies in the form of their incisors. The first upper incisor is always very large indeed ; it looks vertically downwards, is slightly hooked, and has a notch and a second low cusp behind the principal long pointed cusp. The tip of the lower incisor fits into this notch. The lower incisor is also very large ; it lies nearly horizontally, though the point is bent a little upwards. Along its upper edge there are, in most species, three or four small cusps, while its lower border is curiously prolonged outside the bone of the jaw, so as in some measure to encase this latter. The lower incisor is at least one-third as long as the whole alveolar border. The incisor teeth of the shrew would appear to form a very efficient pair of pincers, with which to pick up the minute creatures on which it feeds (Fig. 236).

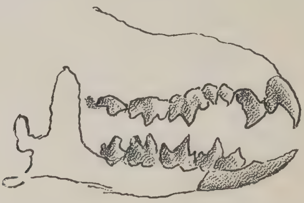

Fig. 236.—Teeth of the common shrew. × 3.

It is difficult to assign a dental formula to the shrews, as the premaxillary suture is lost early, and there is no differentiated canine. Brandt considers that there are four upper incisors, because the fourth upper tooth appears to be in the premaxilla ; but, as Woodward points out, in all Insectivora the relation of the canine to the intermaxillary suture is more variable than in other orders, and, moreover, the gap between the maxilla and premaxilla was so large in a fœtus 1·2 inches long that there were several tooth-germs in the gap. On the whole its probable dental formula is

$$i\,\frac{3}{2}\;c\,\frac{1}{0}\;p\,\frac{3}{1}\;m\,\frac{3}{3},$$

though the upper canine is abnormally situated, and Dobson (5) does not allow the existence of a canine at all. A great deal of doubt has rested upon its milk dentition, some authors claiming that calcified milk teeth existed, and others (Leche) denying the existence of any milk dentition in any stage of suppression.

Woodward, however, examining a fœtus a trifle smaller than Leche's, describes and figures well-differentiated milk tooth-germs to many of the teeth. None of them, however, apparently undergo any calcification, though proceeding so far as the formation of the bell-shaped enamel-organs. All of the incisors, canines, and premolars show traces of these milk tooth-germs, though some are less differentiated than others. The large first incisors show an anomalous condition, namely, a large but not highly differentiated outgrowth on the lingual side of the functional tooth-germ; yet it can hardly be supposed that these large and peculiar teeth are persistent milk teeth.

There is thus a highly reduced milk dentition, none of the germs being known to calcify :—

$$\mathrm{di}\ \frac{2}{-}\ \mathrm{dc}\ \frac{1}{-}\ \mathrm{dpm}\ \frac{3\,4}{4}.$$

The dentition of the **Mole** (*Talpa*) has been the subject of much controversy, the determination of its canines, &c., presenting such difficulty that no less than five different dental formulæ have been assigned to it.

In the front of the upper jaw come three small teeth, the first being somewhat the largest, situated well within the limits of the intermaxillary bone, and are doubtless incisors. But the next tooth, which is of considerable size, also appears to be implanted in the premaxilla, the suture passing across its socket close to the back of its posterior root. The difficulty in accepting this tooth as the true canine was formerly considerable, but is now diminished by the established fact that the relations of this tooth to the suture are variable in insectivores, and that the two-rooted tooth of *Gymnura* is without doubt the canine. The mole has forty-four teeth, and the dental formula usually assigned to it is—

$$\mathrm{i}\ \frac{1\,2\,3}{1\,2\,3}\ \mathrm{c}\ \frac{1}{1}\ \mathrm{p}\ \frac{(1)\,2\,3\,4}{(1)\,2\,3\,4}\ \mathrm{m}\ \frac{1\,2\,3}{1\,2\,3}.$$

M. F. Woodward, however, gives reasons for the belief that $\mathrm{p}\ \frac{1}{1}$ is a persistent milk tooth, in which case its premolar formula should be written thus :—

$$\frac{\mathrm{dpm}1}{\mathrm{dpm}1}\ \mathrm{pm}\ \frac{2.3.4}{2.3.4}.$$

Next behind the canines come three small premolars, and a fourth which is much larger than the others; the three have somewhat simple crowns, consisting of single sharply pointed cusps, whilst the fourth is more molariform.

The first two upper molars are large teeth, bristling with cusps; the third is much reduced in size and simplified in pattern. Woodward calls them of tritubercular or trituberculo-sectorial pattern. (See Fig. 238B.)

In the lower jaw the *four* front teeth are all small, but the fourth or outermost of these incisors is called by some writers the lower canine, because, when the teeth are closed, it passes in front of the upper caniniform tooth. Nevertheless the tooth which does the work of a canine in the lower jaw is the fifth counting from the front; this is a two-rooted tooth, and conforms so closely with the three teeth behind it in configuration that it is obviously only one of these premolars developed to a greater length than the others. It closes *behind* the caniniform upper tooth, so cannot on this ground be called a canine by those who attach homological importance to the term.

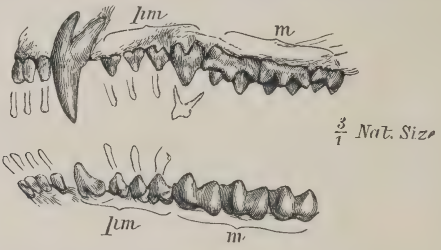

Fig. 237.—Upper and lower teeth of the common mole. The functionless milk teeth are placed above the permanent teeth which displace them, with the exception of the deciduous canine, which is placed too far back, over the first premolar. (After Spence Bate.)

The remaining three premolars are rather small and single-rooted. The lower true molars are of considerable size, and their points are very long and sharp; they have a large heel, so large as to preponderate over the trigon.

The late Spence Bate's paper (¹), valuable as it is in contributing to our whole knowledge of the milk dentition of the creature, does not finally determine the homologies of the canine.

In a mole $3\frac{3}{4}$ inches long he found eight milk teeth on each side of both upper and lower jaws. The milk incisors were about one-twentieth of an inch in length, and one two-hundredth in diameter, and were rudimentary in form, consisting of long thin cylindrical tubes surmounted by slightly expanded crowns. All the milk teeth were of this simple form, save only the last in each jaw, which presented crowns with two cusps, and had their roots to some little extent divided into two.

At the time when these teeth are present, the intermaxillary suture is very distinct, and he had no doubt that the fourth upper milk tooth, the predecessor of the canine, was in the premaxilla.

None of the teeth had fairly cut the gums, and the advanced state of the permanent teeth beside them made it doubtful if they ever did become erupted.

The subject has been reinvestigated by Woodward, who confirms in most respects the accuracy of Spence Bate's account. But in one point he disagrees: he was unable to find (either in clarified jaws or in serial sections) any trace of the deciduous predecessor figured by Spence Bate over the $p\frac{1}{1}$; on the contrary, he found that $\frac{\text{dpm1}}{\text{dpm1}}$ were larger than the other milk teeth, were uncalcified and more backward in their development, but occupying a position corresponding to the reduced milk series. Moreover, there was a lingual bud from the dental lamina, indicating that the tooth-germ under observation was really the milk tooth. He therefore concluded, after an examination of eight specimens, that there is no permanent tooth developed at this place, but that the functional persistent tooth is the milk tooth.

The Insectivora may be divided into groups by the pattern of their molar teeth; the majority present a W-shaped pattern (*Tupaia, Macroscelis, Erinaceus, Sorex, Talpa*), whilst the other group have narrower molars with a V pattern (*Potamogale, Centetes, Chrysochloris*).

The V-shaped teeth, having the early generalised tritubercular form, occur in the Insectivora of Africa, Madagascar, and the West Indies only. It is probable that these are the more generalised types, and that those with the W-shaped molars are the more specialised forms.

The W pattern met with in the molars of Insectivora is well exemplified in the molar of *Urotrichus*.

Mivart (12) held that the patterns of insectivorous teeth were arrived at sometimes by a process of addition, new cusps being formed by elevations of the cingulum, so that the molars bristle with cusps, or by a process of lateral compression, the tritubercular tooth of the Cape mole thus being due to a fusion of the more numerous cusps of such forms as the mole.

The trituberculate forms are said to approach the Jurassic Trituberculata, but, as pointed out by Woodward, this hardly applies to the lower teeth; and it is noteworthy that Woodward finds in two genera (*Centetes* and *Ericulus*) which he has examined that the protocone is the first cusp to appear, both in the upper and the lower jaw.* But though this fact is one which will be gratifying to the advocates of the tritubercular theory, unfortunately it is not true of other genera; for those Insectivora which have more complex upper teeth, with four or five cusps, present a totally different order of appearance of the cusps, and the paracone and metacone appear first. Indeed, it is true of all mammals which have been adequately examined, except the two mentioned, that the paracone appears first in the upper teeth, the protocone coming second or third in order.

This suggests that the homologies as set forth by Osborn and Cope may be incorrect, and that the so-called paracone in the upper molar is the real protocone. If this be so, the awkward dilemma that in the premolars of various mammals the protocone stands outside, and in the molars it stands inside (Scott, [13]), much alike though the last premolar and first molar may be, would be got rid of.

---

* Marett Tims (17) has shown that there is a doubt whether the so-called protocone of the molar teeth in these two genera is in reality the homologue of the protocone in most other mammals.

Dr. Forsyth Major (9) gives strong reasons for not regarding the tricuspid teeth of *Chrysochloris* and *Centetes* as primitive forms, but, on the contrary, as due to reduction, thus reasserting Mivart's view and rejecting those of the advocates of trituberculism so far as these teeth are concerned.

He holds that in the upper molars the three cusps present are certainly not the three cusps of the primitive triangle or trigon, but that the paracone and metacone are fused together, and that the protocone is greatly reduced. He further remarks that in the interpretation of the homologies the cusp, which is really paracone + metacone, has been very generally confounded with the protocone. The lower molar, on the contrary, he regards as consisting essentially of the primitive triangle.

On close examination and comparison with other forms he considers that the so-called tritubercular molars contain more components than the three cusps, and that the three main cusps with which he is dealing have *different homologies* in each of the three orders (Lemuroidea, Carnivora, Insectivora) with which he deals ; hence he regards these sporadic appearances of trituberculism as phenomena of convergence.

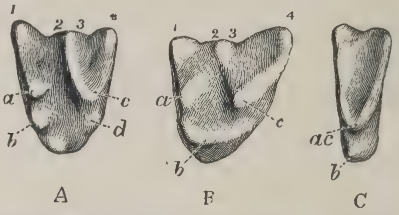

Fig. 238.—Upper molar teeth of (A) *Urotrichus* ; (B) *Talpa* ; (C) *Chrysochloris*. (After Mivart.) The four principal cusps, according to Mivart, are lettered *a*, *b*, *c*, *d*, the other cusps being elevations of the cingulum. Woodward would suggest as their homologies—*b*. Protocone. *a*. Paracone. *c*. Metacone. *d*. Hypocone. He therefore agrees with Mivart that the additional cusps upon the outer border are of less importance than the other or inner four.

In a paper upon the great extinct lemuroid *Megaladapis* (10) Forsyth Major points out that both this creature and *Centetes* have tritubercular upper molars, but that when we come to look at the lower molars we find that in the one it is the front part of the tooth which has undergone reduction, whilst in the other it is the back or heel. Now, according to the advocates of trituberculism, this heel or talon is a secondary and later introduction, but this he entirely disputes.

In support of his argument that the tritubercular molar is a tooth which has been reduced, he cites the fact that the *Viverridæ*, *Centetidæ*, and *Lemuridæ* all have it, though there can hardly be any close generic relationship between them, and there is, moreover, evidence that the reduction sometimes goes well beyond the stage of trituberculism in each of these families, *e.g.*, in the carnivorous *Eupleres*, the insectivorous *Hemicentetes*, and the lemuroid *Cheiromys*.

The structure of the teeth of Insectivora does not call for much detailed notice. Penetration of the enamel by dentinal tubes occurs in some—*e.g. Sorex*.

In the shrews the outer layer of the enamel is deeply pigmented.

The enamel is abundantly entered by dentinal tubes, and there is no sharp line of demarcation at the junction of the two tissues ; the tubes in the enamel often bend abruptly and then resume their original direction.

In *Erinaceus* the tubes do not enter so freely, nor do they run far into the enamel.

In *Gymnura* and *Tupaia* there is little sign of penetration, and the dentinal tubes break up into brushes at the edge of the dentine.

In *Centetes* no penetration occurs, but the enamel is very distinctly laminated.

Teeth of Galeopithecidæ.

This sub-class contains but a single genus, *Galeopithecus*, the common but erroneous name of which is the "Flying lemur" of the Malay region. Its systematic position has undergone many changes. Formerly classed with the true lemurs, it was afterwards included among the Insectivora. Recent researches have shown the advisability of, at any rate provisionally, placing it by itself. The teeth, the genesis of which has been investigated by Deppendorf (4), are somewhat anomalous. The lower incisors are divided by a number of vertical clefts running down through a great part of the length of the crowns, so that they can be compared to combs, or to hands with the fingers slightly separated. What the purpose served by these comb-like teeth may be remains uncertain ; no other animal has similar teeth.

It has been supposed that these teeth are used by the animal in combing its fur, but Leche ridicules this interpretation, deeming it far more probable that they have relation to peculiarities of food. Indeed, one has been observed when eating a banana to suck it through its front teeth, using them as a sieve. Unlike the Insectivora, *Galeopithecus* feeds on fruits and leaves. The so-called canine, which Leche prefers to call the first premolar, is two-rooted, as happens in many Insectivora, but *Galeopithecus* stands almost alone among recent mammals in having i_2 two-rooted ; Leche points out that this is no real distinction from Insectivora, as *Petrodromus* has it two-rooted, whilst in the genus *Erinaceus* it may be found in different species sometimes distinctly two-rooted, sometimes one-rooted.

For *Galeopithecus* Leche (7) gives the following dental formula* :—

$$i\,\frac{2}{3}\ pm\,\frac{3}{3}\ m\,\frac{3}{3}.$$

Galeopithecus has a milk dentition, more complete than most Insectivora, which is late in developing, no teeth being cut in a newly born fœtus, and in one which had a full coat of hair only the points of $\frac{dm_3}{}$ and $\frac{}{di_1\ di_2\ dm_3}$ were through the gums. At this time no succes-

* This formula differs somewhat from that given by Deppendorf.

sional teeth were far advanced, but all the true molars were as far advanced in calcification as the milk teeth, and lay but little deeper in the jaws.

Hence it comes about that in *Galeopithecus* all the molars (except $\underline{m_3}$) are up in place and at work during the persistence of all the milk teeth. This appears to be, so far as it goes, an argument in favour of regarding true molars as homologous with the milk teeth.

There is this further peculiarity, that the so-called $\overline{di_3}$ described, by Owen, is really $\overline{pi_3}$, which is in place, and at work with the milk teeth for a considerable time, $\overline{di_3}$ being a small tooth lost early. The back teeth, both of first (dm) and of second dentitions (pm), present gradated stages of differentiation from the molar type; thus dm_2, contrary to the general rule, differs more widely from the molar type than does its successor; dm_3 and its successor pm_3 are quite alike.

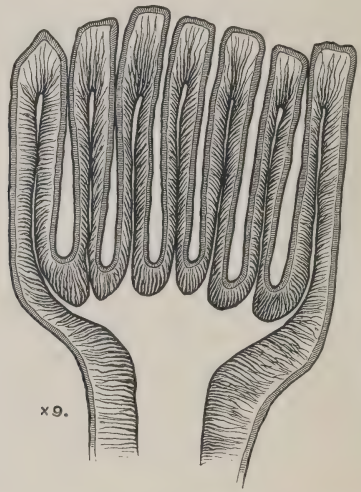

Fig. 239.—Section of lower incisor of *Galeopithecus*, showing arrangement of pulp cavity, dentine, and enamel.

From these peculiarities Leche concludes that the dentition of *Galeopithecus* is an ancient inheritance, and that for a very long time it has been fully adapted to its manner of life.

The enamel of the teeth is very distinctly laminated, but no penetration by the dentinal tubes occurs. Beneath the enamel there is a distinct granular layer, but in no insectivore which has been examined by the author does a granular layer occur in this situation. This is probably correlated with the frequency of penetration of the enamel by a tube system in the latter, and in this respect, as well as in many others, *Galeopithecus* stands somewhat apart from the other members of the group.

The Teeth of Cheiroptera.

CHEIROPTERA	Megacheiroptera	*Pteropodidæ.*
	Microcheiroptera	*Rhinolophidæ.*
		Phyllostomatidæ.
		Emballonuridæ.
		Vespertilionidæ.

The bats, sharply distinguished from all other mammals by the possession of wings, are divided into two groups, respectively insectivorous (*Microcheiroptera*) and frugivorous (*Megacheiroptera*).

The insectivorous bats, by far the most numerous section, are for the most part possessed of small incisors, rather large canines, and premolar and molar teeth which bristle with sharp cusps, and generally present the W-shaped pattern. In fact, in general character, their teeth resemble those of the Insectivora, but the dental formula never exceeds—

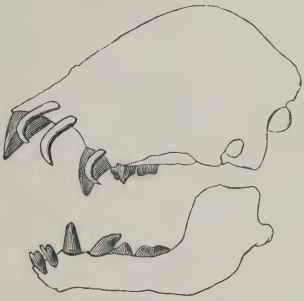

FIG. 240.—Skull of *Desmodus*, showing milk teeth.

$$i\,\frac{2}{3}\;c\,\frac{1}{1}\;pm\,\frac{3}{3}\;m\,\frac{3}{3}.$$

The incisors are sometimes reduced in number, and spaces are left between them; and some, as, for example, the vampire (*Desmodus*), have teeth specially modified to accord with their blood-sucking habits.

This bat has only one permanent incisor on each side, and this is a large but thin and sharp-edged tooth, with which the wound is made; the lower incisors are small teeth with feebly notched edges. The canines are large, and the molar series, which is not required in an animal existing upon blood, is stunted. The molar teeth are, however, sharp, though small, and there is no marked distinction into molars and premolars. The dental formula is—

$$i\,\frac{1}{2}\;c\,\frac{1}{1}\;pm\,\frac{2}{3}\;m\,\frac{0}{0}\;\text{or}\;\frac{1}{1}.$$

The frugivorous bats (of which the *Pteropus*, or flying fox, is an example) have much larger muzzles, and the molar teeth are set with intervals between them.

The dental formula is i $\frac{2}{2}$ c $\frac{1}{1}$ pm $\frac{2}{3}$ m $\frac{3}{3}$, but in some the molar series is reduced below this number.

The incisors are small, and the canines rather large.

Both molars and premolars are of somewhat simple form, long, and compressed from side to side. The outer borders of the crown of the molars are elevated into distinct but not very sharp cusps, which become worn down by use.

The insectivorous character of the presence of many sharp cusps upon the teeth is not to be found in any of the frugivorous bats. All the *Pteropi* have deciduous canines, and four deciduous molars, of simple pointed form, the number of deciduous incisors being very variable.

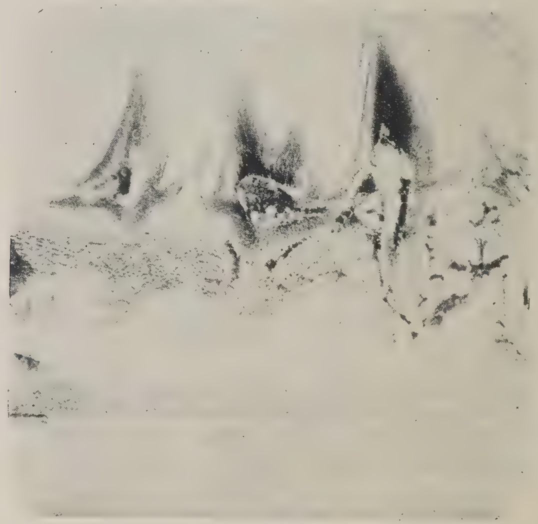

FIG. 241.—Section of molar teeth of *Rhinolophus in situ*, with extreme development of cingula.

The milk dentition of bats has been very carefully and thoroughly investigated by Leche (⁶), and at the present time the *Megadermata* are the only family in which the milk teeth are unknown. The milk teeth are not of much functional importance, as they are shed soon after, if not absorbed before, birth, and they are not therefore implanted in very definite sockets.

In their slight cylindrical elongated roots, surmounted by expanded crowns, these milk teeth often recall those of the mole.

Sometimes the milk teeth are to be found even after the permanent teeth are *in situ ;* in other instances, as, for example, the deciduous molars of *Molossus*, they never cut the gum. The milk dentition of the vampire (*Desmodus*[*]) appears to consist of incisors only, or of incisors and canines, though the absence of observed molars may be due to the fact that they are, as in *Molossus*, shed very early.

It has, near to the front of the upper jaw, six teeth, each of which is very long and slender, with a strongly hooked point (Fig. 240). It has been suggested that these feeble hooked teeth may assist it in holding on to the mother.

In general terms it may be said that the milk teeth of the majority of Cheiroptera do not at all resemble their permanent successors.

An anomalous dentition has been found in a Solomon Island bat, in which the canines, whilst having a long principal cusp, are rendered multituberculate by other cusps at their base, this pattern being more or less repeated in the other teeth (Oldfield Thomas) (14). This seems to indicate that the fruit-eating bats are descended from insectivorous forms.

The bats illustrate well a character of insectivorous dentition in the production of the cingulum to such an extent as to completely cover and protect the gum between the teeth.

The Teeth of Carnivora.

- CARNIVORA
  - C. fissipedia
    - Herpestoidea
      - *Viverridæ*, Civets.
      - *Hyænidæ*, Hyænas.
      - *Felidæ*, Cats.
    - Arctoidea
      - *Canidæ*, Dogs.
      - *Procyonidæ*, Racoons.
      - *Mustelidæ*, Weasels.
      - *Ursidæ*, Bears.
  - C. pinnipedia
    - *Otariidæ*, Sea-lions.
    - *Trichechidæ*, Walrus.
    - *Phocidæ*, Seals.

The animals grouped together under the name of Carnivora are divided into two sections, the Terrestrial (*C. fissipedia*) and the Aquatic Carnivora (*C. pinnipedia*).

The order Carnivora is a very natural one, and its name is, upon the whole, fairly descriptive of the habits of the majority of its members, though there are some creatures included in it which are mixed feeders and others which are purely vegetarian.

The terrestrial Carnivora were formerly classed as "digitigrade" and "plantigrade," a classification exceedingly inconvenient, as it left the greater number of the animals to be classified in the debatable ground between the two extreme types. As a linear classification is impossible, they are frequently grouped around three centres : the *Æluroidea*, or

[*] In a skull of *Desmodus*, in the possession of Mr. R. F. Tomes, the third milk tooth appears to correspond in position to the permanent canine ; the same is the case in the specimen figured by Messrs. Gervais and Castelmain ("Expéd. dans les Part Cent. d'Amérique du Sud").

cat-like; the *Cynoidea*, or dog-like; and the *Arctoidea*, or bear-like Carnivora; and instead of taking the *Felidæ*, or cats, as the type of the group, it is generally considered that the dog tribe are the most generalised forms, and that the cats are an extreme modification in one direction, the bears in another.

The *Cynoidea* comprise the dog, and its immediate allies the wolves and foxes.

The *Æluroidea*, or cat-like Carnivora, comprise the *Viverridæ* (civets), hyænas, and cats.

The *Arctoidea*, or bear-like Carnivora, comprise the *Mustelidæ* (weasels), *Procyonidæ* (racoons), and the true bears.

This arrangement is a convenient one so far as recent Carnivora go, but it breaks down when the extinct forms are included, the *Arctoidea* being connected some with the *Canidæ*, others with the *Viverridæ*. Again, the *Æluroidea* are connected with the *Procyonidæ*.

The connection which undoubtedly exists between the *Cynoidea* and *Arctoidea* is expressed in the classification given above, the *Canidæ* being included among the *Arctoidea*, the Cynoids not being retained as a separate group.

Some fossil forms long known, such as *Hyænodon* (*vide* pp. 59, 364), remained of uncertain position till the rich discoveries in North American deposits revealed a large number of forms which seem to require distinction as a sub-order, to which the name Creodonts has been given. Nevertheless, naturalists are not yet quite agreed as to the limits of this group, Wortman (20), for example, removing from it some forms which Matthew (11) would retain in it, namely, the more immediate ancestors of some of the modern Carnivora. In its more extended sense it undoubtedly contains the ancestors of the Carnivora, and possibly also of the Insectivora, while it is possible that the Condylarthra, the presumed ancestors of the ungulates, may have had a common origin with the Creodonts, as resemblances occur at some points. Creodonts present resemblances also to the carnivorous marsupials, although they have a more complete tooth change, and their relationship to the marsupials is still uncertain. In a large number of Creodonts there is a full number of teeth, which, while adapted to a carnivorous diet, do not show that limitation of the slicing "carnassial" type to a particular tooth in the upper and to another in the lower jaw which characterises the Carnivora. Thus amongst the Hyænodonts, of which *Sinopa agilis* is here figured, the upper carnassial pm4 is sectorial in form, but, with the exception of the last, the true molars are also somewhat sectorial.

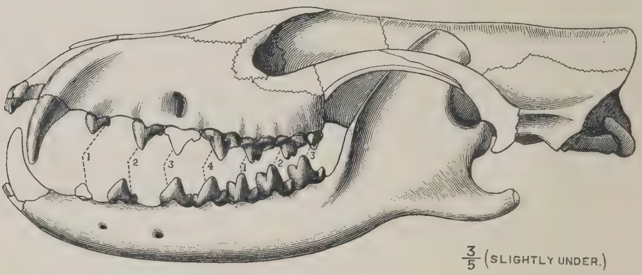

FIG. 242.—*Sinopa agilis*. (After Wortman.)

In the lower jaw the first true molar has a shearing action, but it is smaller than those behind it, which participate in its sectorial character.

Another interesting Creodont form is *Mesonyx*, which had teeth differentiated into incisors, large canines, premolars, and molars.

The incisors were small, and their crowns more or less conical. The upper canines were large, strongly recurved, and sharply pointed, with a considerable diastema in front of them ; the first premolar was single-rooted, but the other three had two roots ; their crowns were compressed, having a principal cusp and a posterior lobe with a cingulum ; the fourth was a little more complex than the others, and was more typically tritubercular.

The upper molars were tritubercular, with a strongly pronounced cingulum at the back, the last molar, however, lacking the postero-external cusp.

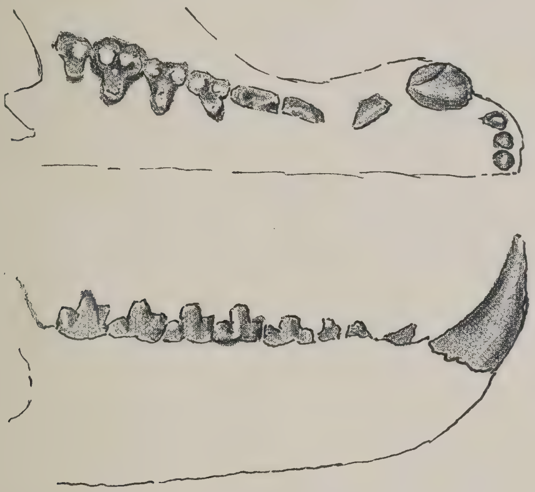

FIG. 243.—Upper and lower dentition of *Mesonyx ossifragus*. (After Cope.) One-third natural size.

The lower premolars and molars are rather simple ; the first is single-rooted and conical, the others having two roots, and a principal cusp, to which are added small anterior and posterior cusps, elevations of the cingulum.

From such a dentition, as Wortman has pointed out, more complex patterns can easily be derived by additions to the front and back of the cones and by the elevation of a cingulum, from which additional cusps can be formed.

Its dental formula was—

$$i\,\frac{3}{2}\;c\,\frac{1}{1}\;pm\,\frac{4}{4}\;m\,\frac{3}{3}.$$

Of the teeth of early Creodonts it may be said that it would not be difficult to imagine how the teeth of all other diphyodont mammals might be evolved from them, whilst Cope ([3]) (and *passim ;* see also Dr. Wortman ([21])) gives an admirable series of extinct genera in which the molar patterns become more complex, and approximate on the one hand to the sectorial teeth of Carnivora, and on the other to the bristling cusps of modern Insectivora.

In others the carnassial or shearing character became even in early times limited to the fourth upper premolar and the first lower molar. These, the *Creodonta adaptiva* of Matthew, Wortman would separate off and group in the same sub-order as modern Carnivora. Thus, according to Wortman's view, the Creodonts proper failed and died out without giving origin to modern forms.

Several authors have drawn attention to the resemblances which exist between the Creodonts and the Polyprotodont Marsupials. The author has compared the minute structure of the teeth in these two groups ([18]) in order to see what light, if any, is thrown upon the problem. The structure of the enamel in marsupials presents characteristics very unusual in placental mammals, the course pursued by the enamel prisms being very simple. The Carnivora also present well-marked enamel characteristics. From his investigations based upon the structure of the teeth alone, the author came to the conclusion (to quote his own words) that the Creodonts " certainly do not stand very near to any marsupial, and that if there be a marsupial ancestor, or an ancestor common to the Marsupials and to the Creodonts, it must be sought considerably further back than any of those examined."

[In a paper dealing with the structure of the enamel in the highly specialised Creodont *Hyænodon*, Thornton Carter ([2]) shows that a penetration of the enamel by tubes," though infrequent," does exist, and that this penetration extends for some distance into the enamel. He also finds the enamel pattern of *Hyænodon* agrees very closely with that regarded by the author as characteristic of the Carnivora.]

In carnivorous animals one tooth on each side of both upper and lower jaws is of considerable length, is sharply pointed, and is called a canine ; the upper canine is separated by an interval from the incisors, the lower canine being received into the vacant space or " diastema " so formed.

The incisors are short, almost always six in number, and stand nearly in a straight line, transversely across the front of the jaw, the outermost upper incisor being sometimes large and more pointed, so as to resemble a small canine.

The incisors and canines may, on the whole, be said to be tolerably uniform throughout the order, but the variations in the premolar and molar teeth are both numerous and interesting.

In the most purely carnivorous members of the order, the *Felidæ*, the true molars are reduced to a minimum, and the hinder ones are thin-edged, " sectorial " teeth. In the bears, on the other hand, some of which are purely frugivorous, the molars are little short of the full typical mammalian number, and are furnished with obtuse and broad grinding surfaces.

The accompanying figure will serve to give the general aspect of the teeth and jaws of a typically carnivorous animal, and to show the great development of the processes for the attachment of muscles, the stout wide arch of the zygoma and the transversely elongated mandibular condyle.

To a particular tooth in the upper jaw, and to its antagonist in the lower jaw, Cuvier gave the name of "carnassial." These, conspicuous in the true flesh-feeders, become less differentiated in the *Arctoidea*, or bear-like Carnivora, and in the bears themselves are indistinguishable from the other teeth, save by a determination of their homologies by a process of comparison with the teeth of intermediate forms.

The carnassial or sectorial tooth in the upper jaw is always the fourth premolar; its crown is divisible into two parts, the one a thin sharp-edged blade, which runs in an antero-posterior direction, and is more or less divided by one or two notches into a corresponding number of cusps; the other part, the "tubercle," is a shorter and blunter cusp, and supported upon a distinct internal root situated at the inner side of the anterior end of the blade. (See Figs. 245.) In those which are most purely flesh-feeders, the "blade" is well developed, and the tubercle of small size, an increase in the tubercular character of the tooth being traceable through those genera which are mixed feeders.

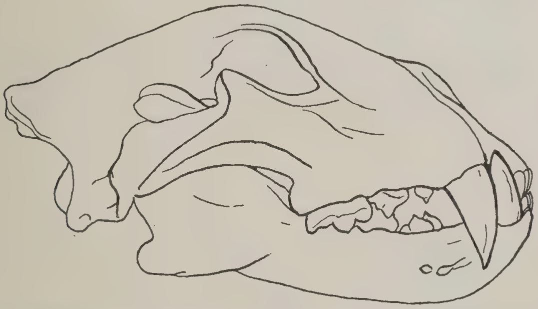

FIG. 244.—Side view of the cranium of a tiger, with the mouth slightly opened to show the relative position of the great canines.

Thus in the bears the tubercle is said to be highly developed; but it is to be noted that the large flattened inner portion of the bear's sectorial tooth is in a more posterior position than the tubercle of a cat's sectorial, and is not supported upon any separate root.

The lower tooth which antagonises the upper carnassial, passing a little behind it, is the first true molar (Fig. 246). In the *Felidæ* it consists of the blade, which is divided into two large blade-shaped cusps, behind which is a very small and rudimentary third division (which in the *Hyænidæ*, for example, is of conspicuous dimensions). In existing Carnivora but one "sectorial" tooth is to be found on each side of the jaws, but in *Hyænodon*, now regarded as a Creodont, which had the full number of forty-four teeth, and in some other extinct tertiary mammals, there were more teeth partaking of this character.

When the blade of the upper carnassial tooth consists of only two cusps, as in the dog, these are the paracone and metacone of the primitive triangle, according to Osborn's interpretation ; the inner tubercle supported on a special root is the protocone.

The blade of the lower carnassial molar consists apparently of the paraconid in front and protoconid behind, the metaconid or postero-internal cusp having disappeared. According to the tritubercular theory, the first change from the primitive trituberculism was the addition of a low heel to the lower teeth, thus forming the tuberculo-sectorial tooth, which in the most specialised forms, such as the *Felidæ*, has disappeared again. It is pointed out by Marett Tims (16) that cusp identification in the *Canidæ* leads into various difficulties, and he hence proposes a fresh identification. He further points it out as remarkable that the "all-important protocone" is so reduced as to have almost disappeared in the upper carnassial tooth, and, according to usual identifications, in some other teeth.

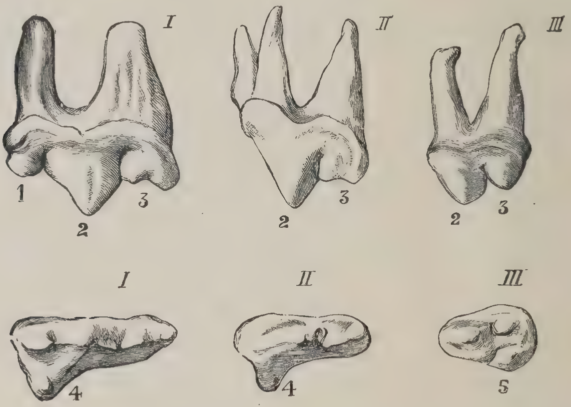

Fig. 245.—Left upper carnassial teeth of Carnivora. I. *Felis*. II. *Canis*. III. *Ursus*. 1. Anterior added cusp. 2. Paracone. 3. Metacone. 4. Protocone. 5. Inner posterior cusp, without distinct root, characteristic of *Ursidæ*.

The accompanying illustrations, which are taken from Flower and Lydekker's "Mammalia," show the modification which the carnassial teeth undergo in various members of the class.

In a general sense we may say that the characters which indicate a pure flesh diet are : the small size of the incisors as compared with the canines and their arrangement in a straight line across the jaw ; the large size, deep implantation and wide separation from one another of the canines ; the reduction in number of the molar series, those that remain being without broad crushing surfaces, in the place of which a pointed or sharp-edged form prevails.

Thus the more numerous the teeth of the molar series, and the broader their crowns, the more likely it is that the creature subsists upon a mixed diet ; and a gradation may be traced even in individual teeth, such as the carnassials, in which a gradual increase in relative size of the internal tubercular cusps of the upper and of the posterior tubercles of the lower teeth may be traced as we pass from the examination of the teeth of *Felidæ* to those of mixed feeders, such as some of the *Arctoidea.*

All of the *Canidæ* have triangular upper molars ; all *Ursidæ* have quadrate upper molars. In the *Canidæ* the inner cusp is anterior ; in the *Ursidæ* it is median in position (Matthew, *loc. cit.*).

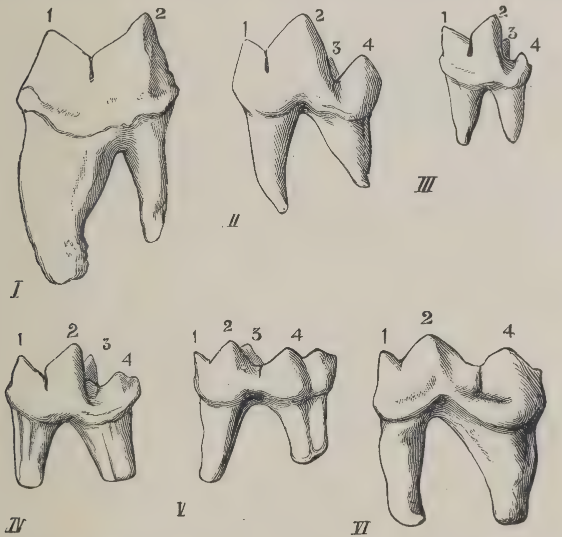

FIG. 246.—Left lower carnassial teeth of Carnivora. I. *Felis.* II. *Canis.* III. *Herpestes.* IV. *Lutra.* V. *Meles.* VI. *Ursus.* 1. Paraconid. 2. Protoconid. 3. Metaconid. 4. Hypoconid. It will be seen that the relative size of the two roots varies according to the development of the portion of the crown they have respectively to support.

It is a familiar observation that immature animals differ less from their allies than do the respective adults, and this is exemplified by the milk dentition of the present order.

With the exception of the *Felidæ*, which have only two lower milk molars, the terrestrial Carnivora, so far as is known, all have the same milk dentition :

$$\text{di}\ \frac{3}{3}\ \text{dc}\ \frac{1}{1}\ \text{dm}\ \frac{3}{3}.$$

The shearing action between the upper and lower carnassial teeth, which serves to cut off chunks of flesh, was not very much developed in the earlier types of Creodonts, and was shared alike by all the molars. But in more specialised types it was chiefly between $\frac{m_1}{m_2}$ or $\frac{m_2}{m_3}$, till in others it came to be between $\frac{pm_4}{m_1}$, as in all recent carnivores.

Herpestoidea.

Viverridæ.—With a dental formula not differing much from the dog and not at all from *Canis primævus*, the *Viverridæ* (civet cats, ichneumons, &c.) approach the more typical carnivores in such points as the thinner and sharper blades of the premolar teeth and the greater relative length and sharpness of the canines.

The dental formula is—

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{2}{2}.$$

At the same time the lower carnassial tooth has no less than six sharply pointed cusps, and it lacks the typical character of a sectorial tooth, while the long pointed cusps of the molars of some *Viverridæ* recall the characters of insectivorous dentitions rather than those of true flesh-feeders; furthermore, there are other *Viverridæ* which are not at all savage, and which subsist on a diet of fruits, eggs, &c., such as the binturong or the *Paradoxurus*, the teeth of which have almost lost the carnivorous character. Little use can therefore be made of the *Viverridæ* as illustrating the transition between the dental characters of the other families of the order; they rather serve to exemplify how within the limits of a single family, with an identical dental formula, the form and size of the teeth may vary so as to adapt its members to different forms of food and habits of life.

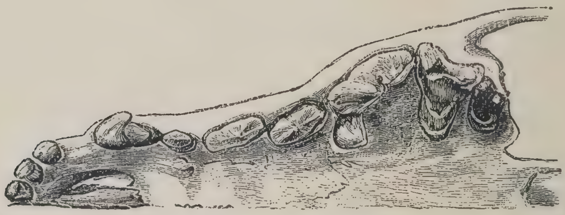

FIG. 247.—Left upper dentition of Indian civet (*Viverra zibetha*). (From Flower and Lydekker's "Mammalia.")

Hyænidæ.—In *Hyæna* the jaw is short and stout; the canines are set far apart, and the teeth of the molar series are reduced in number.

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{3}\;m\,\frac{1}{1}.$$

The incisors are short and stout, but the outermost upper incisor is somewhat caniniform ; the canines are very strong, but are not so long relatively to the other teeth as in the *Felidæ.*

The premolars are all stout pointed teeth, with a very well pronounced basal ridge or cingulum, serviceable in protecting the gums when the creature is crushing up bones. They increase in size from before backwards in the upper jaw, the fourth upper premolar being a well-marked carnassial tooth, with its blade and tubercle.

The lower carnassial or first molar consists of little more than the notched blade ; but the little posterior tubercle, so strongly pronounced in the dog, is in the hyæna distinctly more marked than in the *Felidæ.* (Cf. Figs. 244 and 248.) The only upper true molar is the rudimentary tooth, placed inside the back of the fourth premolar.

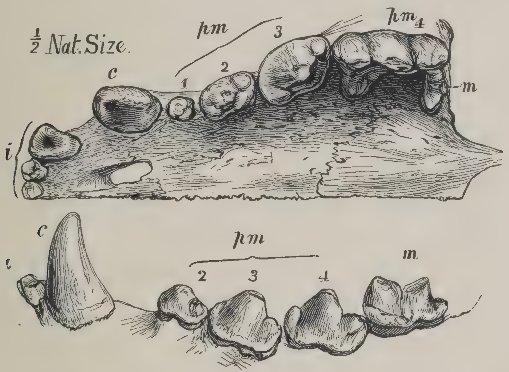

FIG. 248.—Upper and lower teeth of *Hyæna.* The strongly marked cingulum is seen upon the lower teeth. In the upper jaw the fourth premolar (carnassial tooth) has a strong blade, divided into three cusps, and a small tubercle opposite to and within the anterior cusp ; it is a good typical carnassial tooth.

The main feature of the dentition of the hyæna is the great stoutness and strength of the teeth ; they are admirably adapted to the habits of the animal, which feeds rather upon the portions of carcases left by the fiercer Carnivora than upon those which it kills for itself, and consequently bones form a large proportion of its food.

There is a curious hyæna-like animal found at the Cape (of which there are often specimens at the Zoological Gardens) called *Proteles* or aardwolf, in which the teeth of the molar series are quite rudimentary. The incisors (much worn in old animals) and the canines are fairly well developed, the molars and premolars quite stunted.

The deciduous dentition $\left(\text{dm}\ \frac{3}{3}\right)$ is similar to the adult as regards the stunted teeth. It is a cowardly animal, and is supposed to feed on putrid flesh ; it is said to eat young lambs, and to bite the large tails of the Cape sheep, which are remarkable for containing an abundance of semi-fluid fat.

There is also another creature, from Madagascar, named *Eupleres*, which has weak jaws, and a muzzle so thinned down and a dentition so much reduced in power that it was at first regarded as an insectivore. But its teeth are not so rudimentary in form as those of *Proteles*, and they are more numerous, numbering forty.

Felidæ.—The dentition of this family is singularly uniform :—

$$\mathrm{i}\,\frac{3}{3}\;\mathrm{c}\,\frac{1}{1}\;\mathrm{p}\,\frac{3}{2}\;\mathrm{m}\,\frac{1}{1}.$$

Thus the molar series is reduced below that of *Hyæna* by the loss of a premolar in both jaws. The incisors are very short, the canines very large, widely apart, and sharply pointed, with a pronounced longitudinal ridge very characteristic of the *Felidæ ;* the premolars nearest to them are quite short, so that they stand practically alone, and so can penetrate the flesh of living prey more readily.

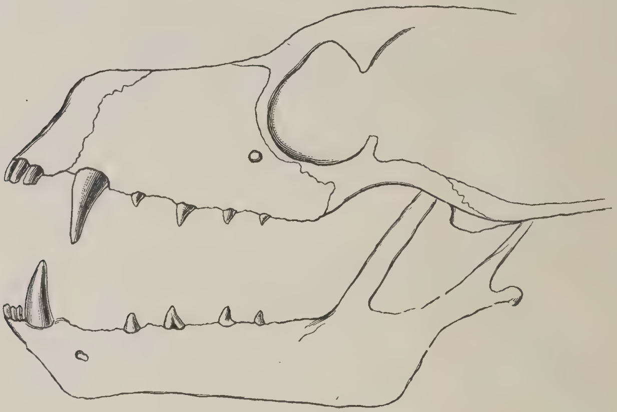

Fig. 249.—*Proteles* (aardwolf).

The first upper premolar (really the second of the typical mammalian dentition) is almost a rudimentary tooth ; the second, a far larger tooth, is sharply pointed ; the last is a well-pronounced carnassial tooth, of which the " blade " is divided by two notches into three sharp lobes, with the middle one of which the " tubercle " is connected by a slight ridge.

The solitary true molar is a very small tooth, placed transversely and within the back of the premolar, so that, looking from the outside, it is not visible at all.

In the lower jaw the carnassial (first molar) is reduced to the " blade " only ; it is divided by a V-shaped notch into two lobes, and the posterior tubercle is hardly represented.

In an extinct feline animal, the *Machairodus*, found in tertiary strata, and very widely distributed in France, Italy, India, Brazil and Buenos Ayres, the first of the premolars left in the upper jaw of *Felis*, and there almost rudimentary (see Fig. 251), has disappeared; the dental formula is thus—

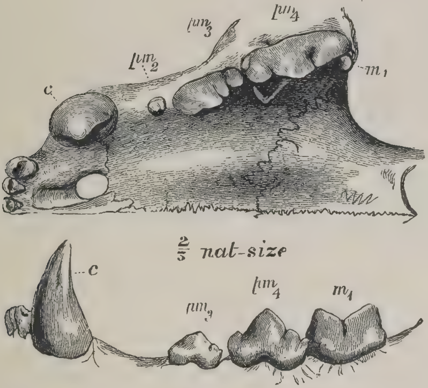

Fig. 250.—Side view of lower and palatal aspect of upper jaw (leopard).

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{2}{2}\;m\,\frac{1}{1}.$$

The upper canines are of immense length, and the ridge of enamel which runs down the front and back surfaces of the teeth is distinctly serrated; hence the name of Saw-toothed Tiger has been given to the animal.

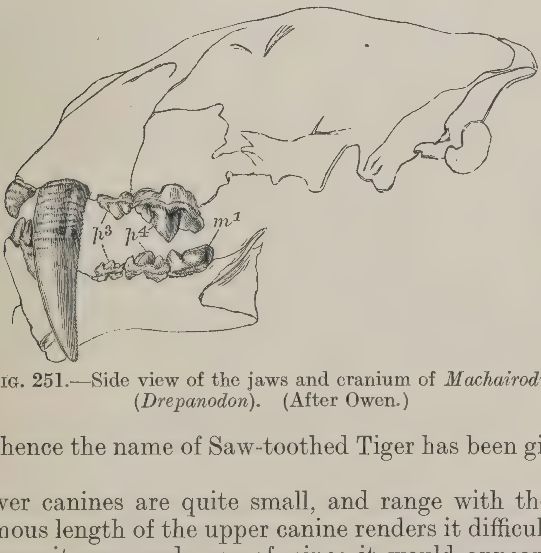

Fig. 251.—Side view of the jaws and cranium of *Machairodus* (*Drepanodon*). (After Owen.)

The lower canines are quite small, and range with the incisors. The enormous length of the upper canine renders it difficult to see in what manner it was made use of, since it would appear as if the mouth could hardly have been opened to an extent sufficient to enable its point to do more than clear the lower jaw.

But it is supposed from the form of the jaws and of the articulation that many of the Creodonts may have been able to open their jaws very widely, and Matthew suggests that *Machairodus* struck rather than bit with its long tusks, a supposition borne out by the feebleness of the processes for attachment of the muscles which close the mouth. It may be fairly assumed that the great contemporary ungulates had thick skins, and that the very long canine was useful for piercing them.

Smilodon, a somewhat similar extinct animal, had a dentition still further reduced, viz.:

$$\mathrm{i}\,\frac{3}{2}\;\mathrm{c}\,\frac{1}{1}\;\mathrm{p}\,\frac{2}{2\text{ or }1}\;\mathrm{m}\,\frac{0}{1}.$$

Professor Cope has described a rich series of extinct cats, mostly from Miocene beds (³). He summarises their characters thus:

"It is readily perceived that the genera above enumerated form an unusually simple series, representing stages in the following modification of parts:—

(1.) In the reduced number of molar teeth.
(2.) In the enlarged size of the upper canine teeth.
(3.) In the diminished size of inferior canine teeth.
(4.) In the conic form of the incisors.
(5.) In the addition of a cutting lobe to the anterior base of the upper sectorial tooth.
(6.) In the obliteration of the inner tubercle of the lower sectorial.
(7.) In the extinction of the heel of the same.
(8.) In the development of an inferior flange at the latero-anterior angle of the front of the ramus of the lower jaw.
(9.) In the development of cutting lobes upon the posterior border of the large premolar teeth.

"The succession of the genera above pointed out coincides with the order of geologic time very nearly.

"The relations of these genera are very close, as they differ in many cases by the addition or subtraction of a single tooth from each dental series.

"These characters are not even always constant in the same species, so that the evidence of descent, so far as the genera are concerned, is conclusive. No fuller genealogical series exists than that which I have discovered amongst the extinct cats."

Arctoidea.

Amongst the Carnivora grouped together by many characteristics as "bear-like," a tolerably complete gradation of character in the matter of dentition may be traced. Some of the group, such as the stoats and martens, are carnivorous; others are mainly herbivorous.

Canidæ.—The dog presents almost the full typical number of teeth, one upper molar (present in an extinct dog-like animal, the *Amphicyon*, and sometimes in *C. cancrivorus*) alone being wanting :

$$\mathrm{i}\,\frac{3}{3}\ \mathrm{c}\,\frac{1}{1}\ \mathrm{pm}\,\frac{4}{4}\ \mathrm{m}\,\frac{2}{3},\ \text{or}\ \mathrm{dm}\,\frac{1}{1}\ \mathrm{pm}\,\frac{3}{3}\ \mathrm{m}\,\frac{2}{3}.$$

Thus in the Cynoidea the number of teeth varies from forty in *Cyon* to forty-six or forty-eight in *Otocyon*, a fox-like animal.

The incisors are small, the outermost being the largest. The upper incisors have, as in a great many Carnivora, a trilobed shape (Figs. 252, 253), the surface of the crown being marked by a transverse groove into which the apex of the lower tooth fits, and the anterior of the lobes thus formed being notched so as to divide it into two. The small lateral cusps of the incisors are, as Tims has shown, entirely of the nature of cingulum-cusps, and are, in his opinion, the homologues of the paracone and metacone of the cheek teeth.

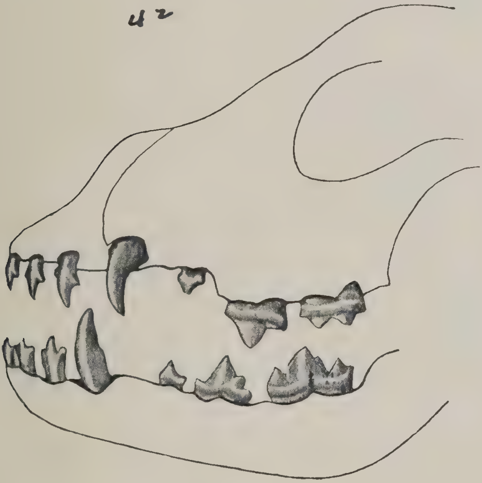

Fig. 252.—Deciduous dentition of *Canis familiaris*. (After Marett Tims, Journ. Linnean Soc., vol. xxv.)

The canines, large and conical, are somewhat compressed from side to side, and have an anterior and posterior sharp ridge ; they are also slightly flattened on their inner surface.

The premolars are flattened from side to side, pointed, increasing in size from before backwards, and have small basal accessory cusps. (See Fig. 254.) The first premolar has no predecessor ; it is a small tooth, and is often lost early ; it is cut considerably before the other premolars, of which pm^4 erupts first* ; and as its follicle appears about the second week, before there is any trace of the follicle of the other premolar teeth, Lesbre regards it as a persistent milk tooth. From this, however, Marett Tims dissents, regarding it as a permanent tooth. The fourth upper premolar is the sectorial tooth, and is very much larger than the third premolar; the blade is well pronounced, and the tubercle small. The fourth lower premolar does not greatly differ from the third. The two upper true molars are blunt, broad-crowned tuberculated teeth, but the second is very small.

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* The peculiarity in the replacement of pm^4 has already been referred to in Chapter XV.

In the lower jaw the first true molar or carnassial tooth has a well-marked blade, which articulates with the blade of the upper carnassial tooth; but towards the posterior border there is a somewhat thick and blunt tuberculate portion, barely represented in the corresponding tooth of the *Felidæ*. This tubercular portion articulates with the broad, flat first upper molar. The second lower molar is smaller, being not one-fourth the size of the first; the third is smaller still; both are blunt-crowned tuberculated teeth (the third lower molar, rudimentary in all dogs, is altogether absent in the *Canis primævus*).

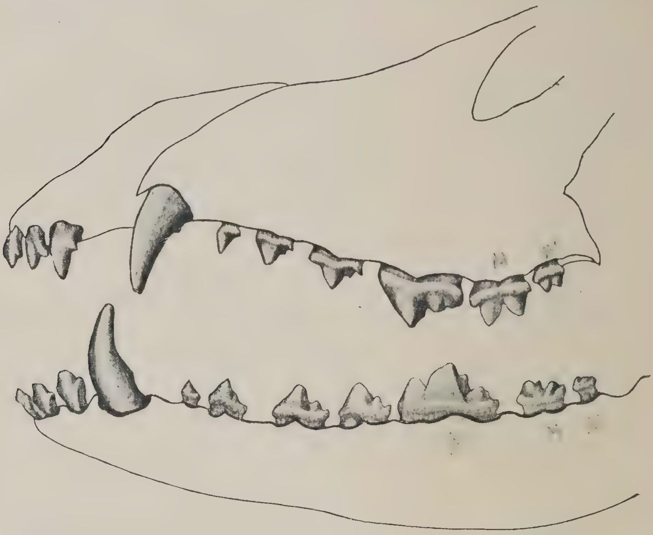

Fig. 253.—Permanent dentition of *Canis familiaris*. (After Marett Tims, Journ. Linnean Soc., vol. xxv.)

The dentition of the dog, closely similar as it is to that of the wolves and foxes, is such as to allow of a considerable range of diet, there being tubercular molar teeth in addition to a full armament of such sharply pointed teeth as are characteristic of flesh-feeding animals.

Thus the *Canidæ*, fairly uniform as they are in dentition, have somewhat different habits: the Arctic fox, a flesh-feeder purely, has a dentition indistinguishable from the North Italian fox, which is reputed to be vegetarian in its diet; the *Canis cancrivorus* of Guiana, which often possesses a fourth molar, eats small mammals, crabs, and also fruit. Hence it is necessary to be very careful in deducing from the character of the teeth what may probably have been the diet of the animal; an approximate idea may often be reached, but the sources of fallacy are sufficiently numerous to render the conclusion uncertain.

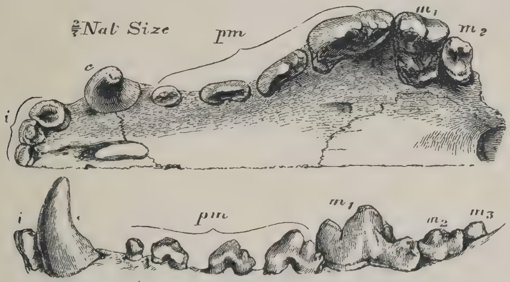

Fig. 254.—Dentition of Australian dog (*Canis-dingo*).

Amongst the various breeds of dogs some slight differences exist. Thus in the long-muzzled races considerable intervals exist between the premolars, as is to some extent seen in *C. dingo* (Fig. 254), while in the short-muzzled races the teeth are in contact and set somewhat obliquely, so as to overlap irregularly, sometimes the hinder edge of the anterior tooth passing outside and sometimes inside the front of the tooth next behind it.

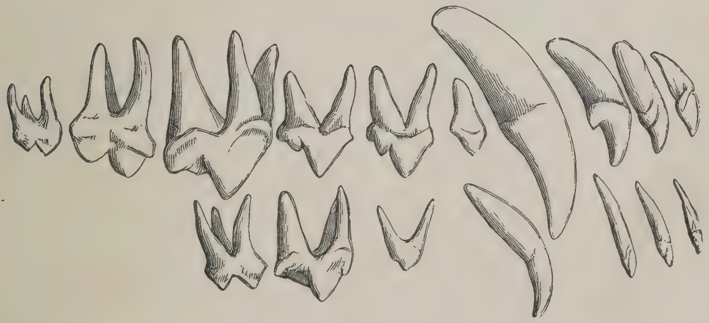

Fig. 255.—Milk and permanent teeth of dog. (After Professor Flower.)

Otocyon, with its extra teeth, is probably a somewhat primitive form, and it is pointed out by Marett Tims that its teeth are more multicuspidate than those of most of the family.

De Blainville mentions that in long-muzzled dogs supernumerary teeth are met with more often than in short, and on the whole it may be said that the teeth are less easily susceptible of modification in size than are the jaws, so that crowding of the teeth is induced by selective breeding aiming at the production of short-muzzled varieties.

Dinocyon gidleyi, a huge extinct dog-like carnivore with a massive skull larger than that of any living carnivore, has been described by Matthew ([11b]).

The **Mustelidæ** (weasels) have the dental formula—

$$i\,\frac{3}{3}\,c\,\frac{1}{1}\,p\,\frac{4}{4}\,m\,\frac{1}{2}.$$

There is a sort of *primâ facie* resemblance to the feline dentition, for the sectorials are very much like those of the *Felidæ*. The first premolar is in many of the *Mustelidæ* rudimentary, and is lost early, but there is not enough known of it to enable us to decide whether it is a persistent milk tooth or a deciduous second tooth. The last tooth in each jaw is a broad-topped tubercular molar, even in the most carnivorous members of the group, while in those which are less so, such as the badger, the molar teeth are very broad and obtuse, the lower sectorial having a very small blade and a very large tubercular posterior talon, so that, without having really lost its typical formation, it comes practically to be a broad grinding tooth.

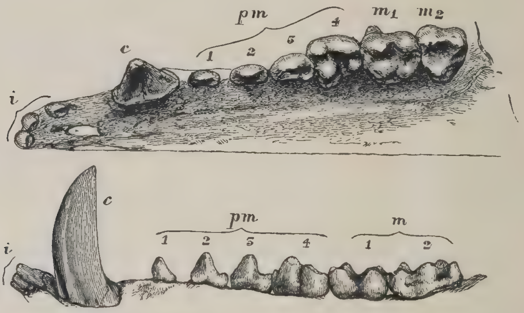

FIG. 256.—Upper and lower teeth of a coatimundi (*Nasua socialis*). The fourth upper premolar (carnassial tooth) has lost its sectorial character by the blade being much less and the tubercle much more developed than in the Æluroidea; there is an additional internal tubercle at the back of the tooth.

In the **Procyonidæ** (racoons and coatimundis, &c.) we have a further departure from the carnivorous character in the increased development of the molar series; the dental formula is—

$$i\,\frac{3}{3}\,c\,\frac{1}{1}\,p\,\frac{4}{4}\,m\,\frac{2}{2}.$$

In the coatimundi, for example, the upper sectorial tooth has a very large "tubercle," and posteriorly to this there is a small additional tubercle; the "blade" has no large or conspicuous thin, flat, sharp edge, but presents two pronounced cusps.

The lower sectorial is no longer recognisable as a carnassial tooth, and all the true molars are broad teeth with four or five cusps.

The canines are very peculiar, those of the upper jaw being very straight and much flattened from side to side, those of the lower jaw strongly curved, and marked by a deep groove near the front of their anterior surface.

Ursidæ.—In the bears the teeth are yet further modified to suit the requirements of mixed or vegetable feeders.

The dental formula is generally—

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{2}{3}.$$

The incisors of the upper jaw present the notch across the crown so common in Carnivora, and the outermost is large and not unlike a canine. The canines are, relatively to the other teeth, not so large as in dogs or *Felidæ*; nevertheless they are stout, strong teeth, upon which the anterior and posterior ridges of enamel are well marked.

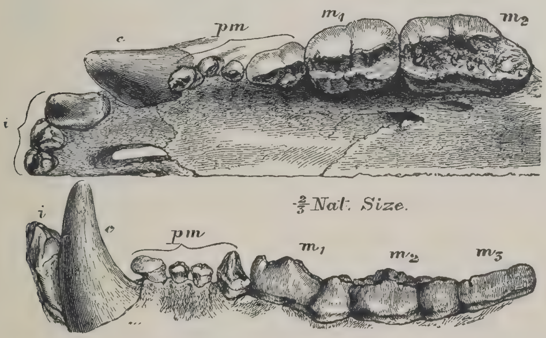

FIG. 257.—Teeth of a bear (*Ursus thibetanus ?*). The figure is drawn from a young specimen, in which the canines have hardly attained to their full length. In this bear the four premolars are all persistent.

The first three premolars are small dwarfed teeth; the first premolar is very close to the canine, and has a crown of peculiar form, produced out towards the canine.

All four of the premolars seldom persist through the lifetime of the animal; the first premolar, however, is rarely (if ever in recent species) lost, the second being the first to fall out, and then the third. As the fourth is never lost, in most adult bears the first and fourth premolars are found with a wide interval between them. The premolars of bears thus form an exception to the rule that when a tooth is lost from the premolars the loss takes place from the front of the series.

The fourth upper premolar (carnassial tooth) retains something of its carnassial character, though relatively to other teeth it is smaller than in the *Felidæ*, the first lower molar very little, save that it is a narrower and more elongated tooth than the other true molars.

The other true molars are square or oblong teeth, raised into blunt tubercular cusps; they vary in different species.

In the sloth bear (*Melursus labiatus*) the incisors are small, and the median pair are lost early. This animal is variously stated to be frugivorous and to feed on ants, the latter probably being the more truthful account.

Carnivora pinnipedia.

The aquatic Carnivora are divided into three families :—

I. The *Otariidæ*, or eared-seals, comprising the single genus *Otaria*, known as sea-lions, or sea-bears. These are the "fur seals" from which sealskin is procured, and they are less removed from the terrestrial carnivora than are the other seals: the limbs are better adapted for walking, there are external ears, &c.

II. The *Phocidæ*, to which family the seals of our own coasts (*Phoca greenlandica*, &c.) and the great proboscis-seals of the southern seas (*Cystophora*) belong.

III. The *Trichechidæ*, or walruses, an aberrant Arctic family consisting of one genus only.

The dentition of the seals is less highly specialised than that of other Carnivora, in some cases approximating to that of homodont cetaceans. This reversion to the homodont type is probably correlated with a fish diet.

The milk dentition is very feebly developed in all seals. In the *Otaria* (fur seal), which of all the seals most approaches to the terrestrial carnivora in other characters, the milk teeth are retained for a few weeks, but in most others they are shed about the time of birth. Thus Professor Flower tells us that in a *Phoca greenlandica* a week old scarcely a trace of the milk teeth was left.

The canines are generally well marked by being larger than the other teeth, but the molars and premolars are very similar to each other, and are simple in pattern.

The teeth of *Otaria*, and of some other seals, become much worn down, and they also seem to become eroded at the level of the gums, as they are often deeply excavated at points which seem unlikely to have been exposed to friction, but the nature of this erosion has not been adequately investigated.

Otaria has a dental formula—

$$i\,\frac{3}{2}\;c\,\frac{1}{1}\;pm\,\frac{4}{4}\;m\,\frac{1\text{ or }2}{1}.$$

The first premolar has no predecessor either in this animal or in the *Phocidæ*.

The incisors, however, vary in number in different groups, while the canines, premolars, and molars are constant.

The common seals (*Phoca*) have a dental formula—

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{1}{1}.$$

The incisors are of simple form, and the outer are the largest. The canine is a strong recurved tooth, with a large root; behind it follows a series of molars, each of which (with the exception of the first) bears a central principal cusp, with a smaller accessory cusp before and behind it. The forms of the crowns vary a good deal in different genera, in some the cusps being much larger, more deeply separated from one another, and recurved; and in others the accessory cusps are multiplied, so that the name of "saw-toothed seal" has been given to their possessor.

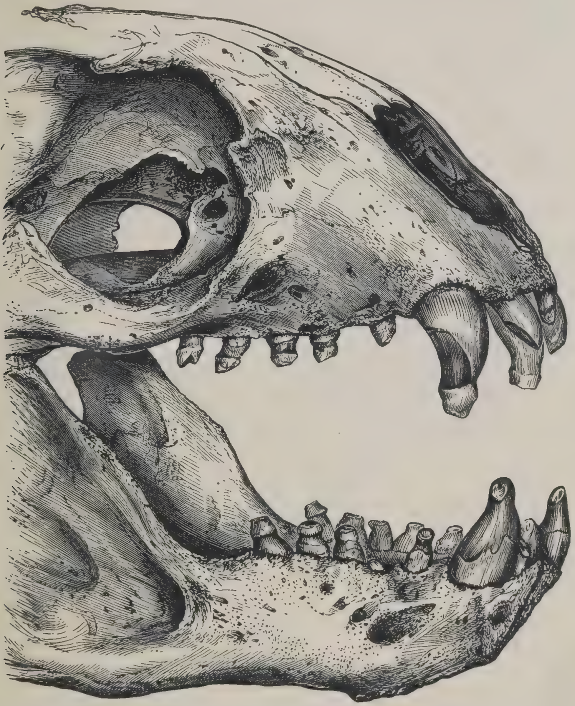

Fig. 258.—Jaws of *Otaria*, in which the teeth are affected by a form of erosion. (After Dr. Murie, "Odont. Soc. Trans.," 1870.)

It has been suggested by Baume that the degree to which the teeth have become simplified perhaps corresponds with the antiquity of the aquatic habits of the genus, those which have taken to the water more recently having retained a greater complexity of tooth crown.

The leopard-seal (*Ogmorhinus*) has teeth with exceedingly long roots disproportionate, one would say, to the necessities of a fish-feeder for firmness in the implantation of its teeth.

In the hooded-seals (*Cystophora*) the incisors are reduced to one in the lower jaw and two in the upper ; the canines are of great size, but the molars are small and simple in form, so as to approximate to the teeth of the Cetacea.

But it is noteworthy that, whereas the Cetacea arrived at a monophyodont and homodont dentition by the suppression of the second dentition, and retain their milk teeth,* the converse is true of the seals.

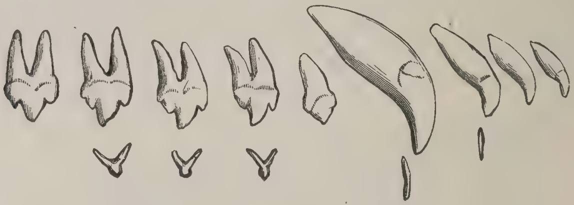

FIG. 259.—Teeth of *Phoca greenlandica.*

The **Walrus** (*Trichechus rosmarus*), an aberrant Arctic form, is possessed of enormous upper canines, which pass down outside the lower lip, and are of such dimensions as to materially modify the form of cranium by the size of their sockets ; they grow from persistent pulps, and are composed of dentine with a thin investment of cement.

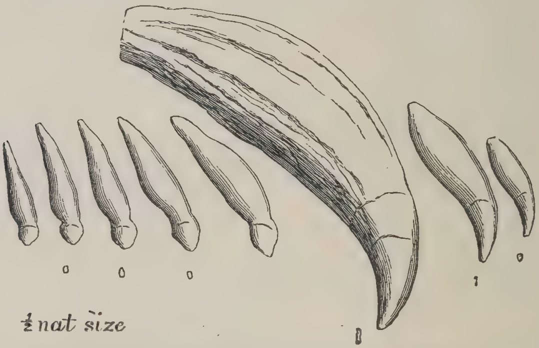

FIG. 260.—Permanent and milk teeth of elephant-seal (*Cystophora proboscidea*).

The great tusks are employed to tear up marine plants and to turn over obstacles, the walrus feeding upon crustacea, and also upon seaweed, &c. ; they are also used to assist the animal in clambering over ice. As they are of almost equal size in the female, they cannot be regarded as weapons of sexual offence, but they are undoubtedly used in the combats of the males.

The largest tusks seen by Nordenskiold were 30 inches in length and 8 inches in circumference; the tusks of the females attain to the same length, but they are much more slender.

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* This statement is open to doubt. Reference is made to this point in Chapter XVIII.

In addition to the great tusks, the walrus ordinarily has a row of four or five teeth, short, simple and worn down to the level of the gums. Of these the one placed immediately within the base of the great canine is in the intermaxillary bone, and is hence an incisor. The ordinary dental formula is given by Flower as—

$$i\,\frac{1}{0}\,c\,\frac{1}{1}\,p\,\frac{3}{3}.$$

But there is some difficulty in assigning a definite dental formula, for in front of the solitary incisor are often the sockets (or even the teeth themselves) of two others, which are for various reasons rather to be regarded as non-persistent teeth of the permanent set than as milk teeth; and there are small teeth sometimes to be met with behind the molars, which also seem to be rudimentary permanent teeth.

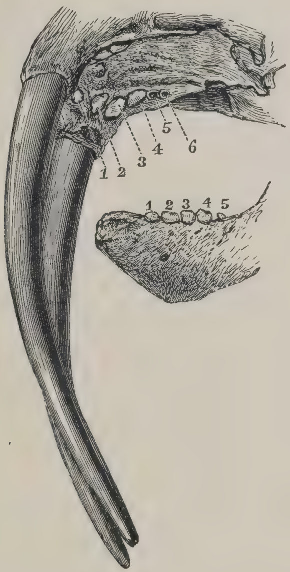

Fig. 261.—Side view of upper and lower jaws of a walrus (*Trichechus rosmarus*). The upper jaw has been tilted a little to one side, in order to bring into view the molar teeth at the same time with the long tusks. The determination of the teeth being open to question, they have been simply numbered.

In young specimens the dentition is—

$$i\,\frac{3}{3}\,c\,\frac{1}{1}\,pm+m\,\frac{5}{4}.$$

The teeth above alluded to may persist through life, and probably often do; but they are sure to be lost in macerated skulls, as they have but little socket. Of the milk dentition four teeth have been traced in each jaw; they are rudimentary, are lost about the time of birth, and correspond in position to the more largely developed teeth of the adult. Hence the question if those small rudimentary teeth above alluded to are to be regarded also as milk teeth, which are long retained, or as rudimentary permanent teeth; at present this requires further elucidation.

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CHAPTER XVII.

THE TEETH OF EDENTATA, RODENTIA AND TILLODONTIA.

THE TEETH OF EDENTATA.

Edentata	Tubulidentata	*Orycteropodidæ*, Aard-varks.
	Pholidota	*Manidæ*, Pangolins.
	Xenarthra	*Bradypodidæ*, Sloths. *Myrmecophagidæ*, South American Ant-eaters. *Dasypodidæ*.

The term Edentata was applied to the animals of this order to indicate the absence of incisors (teeth in the intermaxillary bone). Though this is true of most of them, a few have some upper incisors, the suture between the maxilla and the premaxilla passing, in some armadillos, behind the first upper tooth, but the central incisors are in all cases wanting. It is also stated that in *Dasypus sexcinctus* there are some rudimentary teeth in the incisor region which never cut the gums.

[In *D. novemcinctus*, Martin (6) found that there were from three to five upgrowths of the oral epithelium at the posterior end of the premaxilla, which lost their connection with the oral epithelium, and formed detached cellular masses precisely similar to the "concentric epithelial bodies" described by Marett Tims in the guinea-pig. Martin agrees with the latter writer in interpreting these structures as tooth-vestiges. In the lower jaw he found evidences of five or six incisors, which do not become functional.]

Some edentates are quite edentulous; this is the case in the South American ant-eaters (*Myrmecophaga* and *Cyclothurus*), in which the excessively elongated jaws cannot be separated to any considerable extent, the mouth being a small slit at the end of the elongated muzzle. Marett Tims has shown (12) that the elongated muzzle is associated with greatly elongated lips, the free margins of which have fused together, leaving only a small circular mouth at the extremity of the muzzle. The insects are by this means prevented from escaping at the sides of the mouth, between the lips. Food is taken in by the protrusion of an excessively long, whip-like tongue, which is covered by the viscid secretion of the great submaxillary glands, and is wielded with much dexterity. The *Manis*, or scaly ant-eater, is also edentulous; and it is said by Max Weber (16) that the reduction has gone so far that no dental rudiments could be detected.

Röse,* however, examining Max Weber's sections, came to a different conclusion, and is of opinion that the slight epithelial thickening which he finds in them is to be interpreted as the preliminary to the formation of a tooth-band, and in the lower jaw he has found it to grow in to form a small rudimentary tooth-band (8). It, however, goes no farther, and the appearances would not be very significant but for the inherent probability that some remnants of original tooth formation would linger behind, on the ground that edentulous mammals are almost certainly degenerated forms which have lost their teeth.

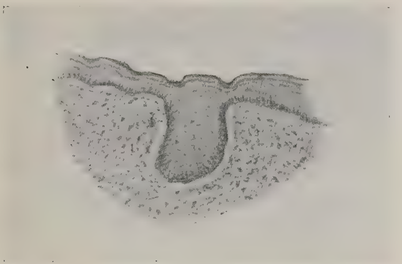

FIG. 262.—Lower jaw. Ingrowth of epithelium in outer incisor region. Tooth-vestige of Röse. (After Tims, Journ. Anat. and Phys., vol. xlii.)

In *Manis javanica* Marett Tims (12) has confirmed Röse's conclusion (*loc. cit.*) by finding what he considers to be a quite definite tooth-vestige which he regards as that of the outermost upper incisor (Figs. 262, 263). He also finds more posteriorly a number of curious structures of doubtful nature. Microscopically they somewhat resemble developing hair, but their roots are implanted in the substance of the jaw, and are growing towards the alveolar margin. They closely resemble the imperfect enamel-organs seen in certain fish. Marett Tims, from a full consideration of all the facts, believes

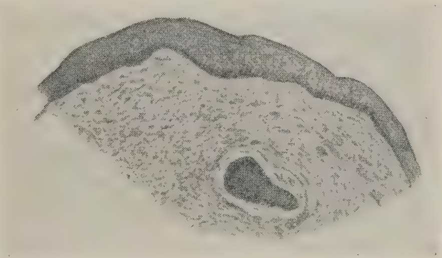

FIG. 263.—The deepest extremity of the same. Three sections behind preceding figure. The intervening sections show the downgrowth to be continuous. (After Tims, Journ. Anat. and Phys., vol. xlii.)

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* The species examined by Max Weber and Röse was *M. tricuspis*.

that these structures must be regarded as the last vanishing remains of teeth (Fig. 264). There are as many as thirteen or fourteen of these structures in the lower jaw on each side.

Whilst they are mostly monophyodont, at least one armadillo has a succession of teeth, and so has the aberrant *Orycteropus* or aardvark. Leche states that he has found in *Bradypus* a calcified but aborted predecessor to one tooth in front of the mouth, and Röse states that in all (*Dasypus novemcinctus*, *D. villosus*, *D. hybridus*, and *Orycteropus*) which have been microscopically studied indications at least of successional germs have been seen.

The Edentata belong to the homodont section of mammalia, but in some sloths certain teeth are more largely developed than others, so that there are teeth which might be termed canines. [According to Martin, this statement does not hold good for *Dasypus novemcinctus*, the first, second and eighth teeth of the lower jaw being single-cusped, the intervening teeth of the series being bicuspid with a higher lingual and a lower labial cusp.] The teeth are, however, usually of simple form, and do not differ in any material degree in different parts of the mouth, except only by their size (to this the caniniform tooth of the two-toed sloth is an exception). They are all of persistent growth, and therefore no division of parts into crown, neck, and root is possible. They consist generally of dentine and cement, with sometimes the addition of vaso-dentine, into which latter tissue the central axis of the pulp is converted ; while in some members of the order other peculiarities of structure exist : thus in the *Orycteropus* (Cape ant-eater) dentine like that of *Myliobates* is found ; in the *Megatherium* hard dentine, a peculiar vaso-dentine, and vascular cementum co-exist, [and in *Dasypus novemcinctus* the dentition is of the ordinary tubular variety in the more posterior

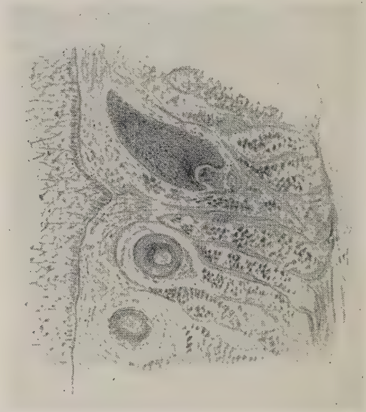

Fig. 264.—Tooth-vestiges (?) highly magnified. (After Tims, Journ. Anat. and Phys., vol. xlii.)

teeth, but in those more anteriorly situated the dentine tends towards the cellular type, with obliteration of the pulp cavity (Martin). The presence of enamel had previously been shown by Spurgin (9) in an embryo of the same species.]

Enamel has not been seen upon the teeth of any existing edentate, but the author found some years ago that the tooth-germs of the nine-banded armadillo were provided with enamel-organs. This, however, proves nothing, for he showed the presence of enamel-organs to be universal and quite independent of any after-formation of enamel (14). Röse, however, whilst confirming the absence of true enamel, holds that there is a mere glaze of structureless material (schmelzoberhautchen). And it is pointed out by Leche that in *Tatusia* the specialisation of the enamel-organ goes on to the point of the internal epithelium becoming transformed into columnar ameloblasts, but that in *Bradypus* these cells remain rounded. It may be supposed, both from palæontological and developmental evidence, that the Edentata, so far as teeth are concerned, are degenerated forms; the shape of the tooth-germs and of the unworn teeth suggests that they branched off from an early triconodont stage with numerous molars, diphyodont, heterodont and furnished with enamel. They have suppressed the milk heterodont dentition, so that they are now more or less completely monophyodont, and have established a homodont second series.

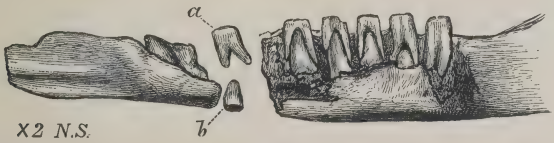

FIG. 265.—Lower jaw of a young armadillo (*Tatusia peba*), showing the milk teeth (*a*) in place, and their successors (*b*) beneath them. From a specimen in the Museum of the Royal College of Surgeons.

Armadillos.—The teeth of the nine-banded armadillo (*Tatusia peba*) will serve to illustrate the character of the dentition of the class. They are seven in number on each side of the jaw, of rounded form on section, and those of the upper and lower jaws alternate, so that by wear they come to terminate in wedge-shaped grinding surfaces; before they are at all worn they are bilobed, as may be seen in sections of the tooth-germs.

In the accompanying figure (Fig. 265) the milk teeth are represented, and beneath them their permanent successors. The divaricated bases of the milk teeth are due to the absorption set up by the approach of their successors, and not to the formation of any definite roots. Successional teeth have been detected in this armadillo only (except in *T. kappleri*, which is, perhaps, a mere variety).

In the armadillos the teeth are always of simple form and about thirty-two in number, except in *Priodon*, which has as many as a hundred teeth, a number altogether exceptional among mammals. The axis of the tooth is occupied by a sort of secondary dentine in which the tubes run almost longitudinally and are gathered into bundles.

Sloths have fewer teeth than armadillos, and these softer in character, the axis of vaso-dentine (which is well pronounced and sharply marked off from the peripheral dentine) entering more largely into their composition, and forming as much as half the bulk of the tooth.

The two-toed sloth has $\frac{5}{4}$ teeth in each side of the jaws, and these are nearly cylindrical in section and of persistent growth, while in the region usually occupied by a canine there is a tooth much longer and larger than the rest.

Sir W. Flower and Pouchet and Chabry had failed to discover any succession of teeth in the sloths, and the author examined microscopically the jaws of a fœtal *Cholœpus* and one other sloth in which the teeth were but little calcified, and failed to detect any indication of a second set of tooth-germs. Semon also, though finding two rudimentary incisors in the lower jaw of a sloth, has seen no evidence of any succession. The probability is, therefore, that they are truly monophyodont, unless Leche, examining younger embryos than he has yet obtained, should find further traces of an antecedent dentition.

The true ant-eaters are all edentulous, but Röse has seen very faint indications of a possible tooth-band in *Myrmecophaga*.

The **Orycteropus,** or **Cape Ant-eater** (Aard-vark), the peculiarities of whose teeth have already been alluded to, has about thirty-six teeth in all; but these are not all in place at one time, the smaller anterior teeth being shed before the back teeth are in place. Pouchet and Chabry found a rudimentary tooth in the incisor region.

They are cylindrical teeth of persistent growth and simple form, and, like the teeth of the armadillo, interdigitate with one another.

The affinities of the aard-vark are very uncertain; it is grouped with the Edentata, but it is a very aberrant form, not only differing strongly in the structure of its teeth, which resembles that of *Myliobates,* but in other zoological characters as well. Oldfield Thomas has discovered that it also displays a succession in its teeth (10).

The milk teeth are rudimentary and probably quite functionless. and though they become calcified, it is doubtful if they ever cut the gum. Unlike the permanent teeth, they are not of the persistent growth type, but one tooth at least, the most posterior, has two distinct roots. There are no teeth in the premaxilla, but seven have been found in the maxilla, and four on each side of the mandible.

In structure they present an approximation to that of the functional teeth, and the last is molariform, the others being simple cones.

So that *Orycteropus* retains traces of descent from a diphyodont and heterodont ancestor.

In former ages many edentates existed of much larger size, and the teeth of some of the gigantic extinct edentates were a little more complex in form and structure ; thus the teeth of the *Glyptodon* were divided by longitudinal grooves, which in section rendered it trilobed, and the teeth of the *Megatherium* were likewise marked by a longitudinal furrow, and presented greater complexity of structure.

In their persistent growth, uniformity of shape, and absence from the intermaxillary bone, they strictly conformed with the teeth of recent Edentata.

Amongst the Eocene fossils from the Puerco region, Cope has found forms which connect the Edentata with other mammals so far as their dentitions go.

Thus *Hemiganus* (Cope) had certainly one, if not two, upper incisors with enamel on their anterior faces only, and with closed roots, and a very large canine, with enamel all over its crown, though thin upon the back. The lower canine had closed roots and enamel limited to the front. (It may have been worn off the back.)

Psittacotherium had two incisors above and one below ; the enamel was limited to the front on the upper incisor, which became worn to a chisel edge, and the lower incisor had enamel all over, but very thin on the back. The canines also had enamel on the front, and, like the incisors, had closed roots, though they went on growing long. Thus in *Psittacotherium* (Cope) the external lower incisors had disappeared, and a more or less rodent type of dentition had become established.

In *Calamodon,* the lower canines were very large, scalpriform, with thick enamel on the front and none on the back, and of persistent growth. Premolars and molars somewhat hyposodont, with elongated roots, but not of persistent growth, and possessed of enamel in bands, thick cementum taking its place where it was deficient.

In *Stylinodon* (Cope) the molars were cylindrical with long bands of enamel, and were of persistent growth. According to Wortman (^{18}), these primitive Edentata (*Ganodonta,* a disputed term) in their earlier forms had teeth with closed and divided roots, and enamel more or less complete ; in later forms the teeth became hyposodont, without roots, of persistent growth, and with enamel limited to vertical bands, while incisors were present in both jaws.

The Teeth of Rodentia.

RODENTIA { Duplicidentata—Hares and Rabbits.
Simplicidentata—All other Rodents.

The animals belonging to this sharply defined order are scattered almost all over the world. The island of Madagascar is, however, remarkable for being almost without indigenous rodents at the present day, though squirrels were numerous during the Miocene period. Indigenous rodents are also absent from Australia, two facts which are of no small interest to the student of odontology. For in each of these areas, out of the creatures which are there (in the one lemurs, in the other marsupials) there has arisen a form so modified as to mimic and take the place of the true rodents, viz., the *Cheiromys* in Madagascar and the wombat in Australia.

In past times, however, a large number of animals, widely apart from one another in their affinities, have more or less approximated to the characteristics of a rodent dentition, and as this adaptive resemblance would give to them advantages in getting access to food which was denied to animals with relatively blunt and weak front teeth, it is possible that some of these may have left descendants, and that hence the existing rodents may have sprung from more than one stock.

Matthew (5) has described an extinct rodent (*Ceratogaulus*) which is peculiar in possessing horn cores situated on the nasal bones. Others which resemble it in dentition are without the horn cores. They all have one tooth (pm ^{4} ?), exceedingly enlarged.

The species of rodents are exceedingly numerous, and the great majority of them are of small size; the aquatic Capybara is by far the largest of recent rodents.

An average rodent dentition would be—

$$\text{i}\,\frac{1}{1}\ \text{c}\,\frac{0}{0}\ \text{pm}\,\frac{1}{1}\ \text{or}\,\frac{0}{0}\ \text{m}\,\frac{3}{3};$$

as extremes the **Hare** has—

$$\text{i}\,\frac{2}{1}\ \text{c}\,\frac{0}{0}\ \text{pm}\,\frac{3}{2}\ \text{m}\,\frac{3}{3},$$

and *Hydromys*—

$$\text{i}\,\frac{1}{1}\ \text{c}\,\frac{0}{0}\ \text{pm}\,\frac{0}{0}\ \text{m}\,\frac{2}{2}.$$

In general features the dentitions of the numerous species comprising this order are very uniform. The incisors (save in the hares and rabbits, in which there is an accessory small pair immediately behind the large ones) are reduced to four in number, are of very large size, and grow from persistent pulps. The jaws for some little distance behind the incisors are devoid of teeth, while beyond the interval (*diastema*) the cheek teeth, generally not more than four in number, are arranged in lines which diverge slightly as they pass backward. The large scalpriform, or chisel-like incisors, extend far back into the jaws and are much curved, the upper incisors, in the words of Professor Owen, forming a larger segment of a smaller circle than the lower, which are less curved. The length and curvature of these incisors relieve their growing pulps from direct pressure, which come to be situated far back in the jaw, the open end of the lower incisor, for example, being in many species actually behind the last of the molar teeth. The nerve going to supply the persistent pulps is of considerable size, and, owing to the open end of the tooth having formerly occupied a more anterior position in the jaw, runs forward beneath the tooth, and then bends abruptly backwards to reach the tooth pulp. In many rodents the enamel of the front of the large incisors is stained of a deep orange colour; this colour is situated in the substance of the enamel itself.

The scalpriform incisors terminate in cutting edges, the sharpness of which is constantly maintained by the peculiar disposition of the tissues of the tooth.

The investment of enamel, instead of being continued round the whole circumference of the tooth, is confined to its anterior and lateral surfaces, on the former of which it is thickest.

It is, however, stated that the enamel-organ is continued round the roots, so that the connective tissue bundles by which attachment to the cementum is made have to grow through it to take their hold (v. Brunn).

[The apex of the primitive tooth (albino rat) is formed of a variety of secondary dentine—the osteo-dentine of Tomes—which is softer than true dentine. After eruption this is worn away; but as the tooth continues to grow, the apex of the pulp chamber is continually filled in by the formation of this osteo-dentine about 1 mm. from the occlusal surface, the soft parts of which in time disappear (1).]

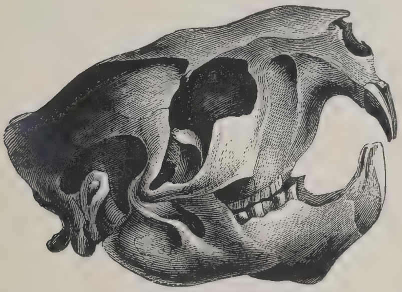

FIG. 266.—Side view of skull of a rodent, giving a general idea of the dentition of the order.

It is said by Hilgendorff (3) that the incisors of hares differ from those of all other rodents in having enamel all round them, although it is very thin at the back. It is doubtful whether the thin clear layer at the back of the tooth is enamel, and the author is disposed to regard it as cementum, the more so as it seems to be continued a little way upon the enamel, and in very young teeth the large cells of the enamel-organ are confined to the anterior surface.*

When a rodent incisor has been exposed to wear, the anterior layer of enamel is left projecting beyond the level of the dentine, and this arrangement results in a very sharp edge being constantly maintained. The dentine also is harder near to the front of the tooth than towards the posterior surface. It is said that no enamel was ever present on the tip of the incisor.

A thin external coat of cement is found upon the back of the tooth, but is not continued far over the face of the enamel. In the marsupial wombat this layer of cement is continued over the whole anterior surface of the scalpriform incisors.

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* Cf. E. G. Betts, "Observations on the Teeth of certain Rodents," Trans. Odontological Society, May, 1884.

Behind the great incisors in all rodents there comes a wide gap, no canines and but few premolars being present; this gap leaves the growing incisors free scope in use.

In many the lips dip deeply into this gap, and so separate the mouth into an anterior and posterior chamber. Possibly this is advantageous in preventing the chips of such a thing as a nutshell from passing back into the mouth.

The grinding teeth are not very numerous; the mouse family have usually $\frac{3}{3}$; the porcupines have constantly $\frac{4}{4}$ and the hares $\frac{6}{5}$; the Australian water-rat (*Hydromys*) is altogether exceptional in having so few as $\frac{2}{2}$. Observation has established that the last three of the teeth are always true molars, and that when there are more than three the rest are premolars.

A good deal of diversity exists in the premolar and molar teeth.

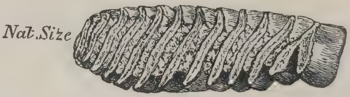

FIG. 267.—Molar of Capybara, showing the transverse plates of dentine and enamel united to one another by cementum.

In rodents of mixed diet, such as the common rat, the back teeth are coated over the crown with enamel, which nowhere forms deep folds, and they have distinct roots, *i.e.*, are not of persistent growth. In aged specimens the enamel is consequently worn off the grinding surface of the crown, which comes to be an area of dentine, surrounded by a ring of enamel. The molars of the rats have some sort of resemblance to minute human molars.

But in those whose food is of a more refractory nature the molars, like the incisors, grow from persistent pulps (as is exemplified in the Capybara here figured), and their working surfaces are kept constantly rough by the enamel dipping in deeply from the side of the tooth, as may also be seen in the common water-rat. The inflection of enamel may be so deep as to divide up completely the areas of dentine, the result being a tooth like that of the Capybara, which is composed of a series of plates of dentine, or " denticles," surrounded by layers of enamel, and all fused together by the cementum. The result of this disposition of the structures is that the working surface is made up of enamel, dentine, and cementum, three tissues of different hardness, which wear down at different rates, and so maintain its roughness. Various intermediate forms of the molar teeth are met with; thus there are some in which complexity of the surface is maintained by folds of enamel dipping in for a little distance, but which, nevertheless, after a time form roots, and cease to grow. In general terms it may be said of the rodents, just as of ungulates, that the brachyodont bunodont type is the older, and that the laminated hypsodont type is of later acquisition. And, as is pointed out by Forsyth Major (5), the young, unworn, laminated hypsodont molar is at first tuberculated or bunodont, and the brachyodont tubercular molar, when worn down, partakes more or less completely of the laminated pattern on its grinding surface. When the molar teeth grow from persistent pulps, they are always curved, like the incisors, with the effect of relieving their pulps from direct pressure during mastication; and the last remains of the pulps are converted into secondary or osteo-dentine, which thus forms the central axis of the incisors, or molars, as the case may be. In this tissue vascular tracts sometimes exist, but the secondary dentine is altogether small in amount, the formation of true dentine going on till the pulp at that particular point is almost obliterated.

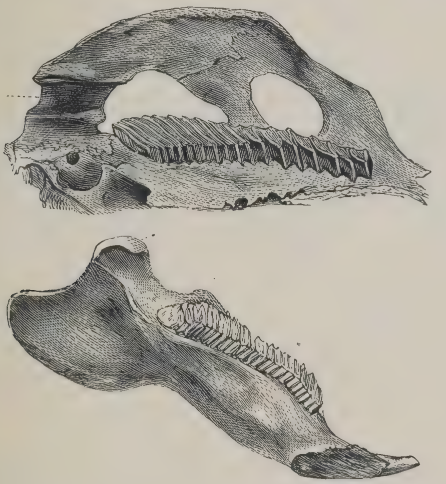

FIG. 268.—Condyle and glenoid cavity of the Capybara, showing their longitudinal direction.

As has already been mentioned, when the molar series consists of more than three teeth, those anterior to the three true molars are premolars, but they do not differ materially in size or form from the true molars.

The forms of the condyle and of the glenoid cavity in rodents are characteristic; they are elongated in an antero-posterior direction, so that the range of backward and forward motion, made use of in gnawing, is very considerable. The *Leporidæ* are exceptional in having more lateral play than most rodents. The power of the teeth is marvellous; rats, for example, will sometimes gnaw holes in water-pipes, or in gas-pipes, in which they have heard water bubbling.

The general character of a rodent's dentition may be illustrated by a description of that of the *Capybara*.

The incisor teeth are quadrilateral, wider than they are deep, and are slightly grooved on their anterior surfaces.

There are four grinding teeth on each side, of which the first three are small with few cross plates of dentine and enamel, but the fourth is a very complex tooth with twelve or more such plates, which are fused into a solid mass by cementum.

This tooth being one of persistent growth, there is no common pulp cavity, but each plate has its own.

It has already been mentioned (p. 191) that the dentinal tubes at that part of the rodent's incisor which has come into use are much smaller than those near to its growing base, thereby proving that they have undergone a diminution in calibre at a time subsequent to their original formation. Near to the surface actually in wear they become cut off from the pulp cavity by the conversion of what remains of the pulp into a laminated granular mass, so that the dentine exposed on the surface must be devoid of sensitiveness, and the contents of the dentinal tubes must have presumably undergone some change. But what the nature of the change in the contents of the dentinal tubes which have ceased to be in continuity with a vascular living pulp may be there are no observations to indicate.

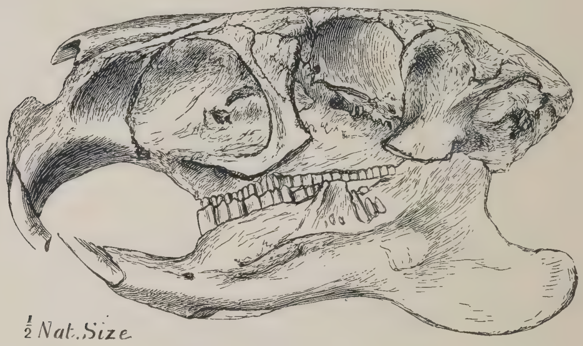

Fig. 269.—Cranium of Capybara.

As was shown by Sir J. Tomes (13), the enamel of rodents is peculiar, and some little diversity in the arrangement of the prisms exists in different families of the order, their character being in many cases so marked that it is often possible to correctly refer a tooth to a particular family of rodents after simple inspection of its enamel.

In general terms it may be said that the enamel is divided into two portions, an outer and an inner portion (this is true of all save the hares and rabbits), and that the enamel prisms pursue different courses in these two portions.

Thus, in the enamel ot the beaver, in the inner half, nearest to the dentine, the prisms of contiguous layers, as seen in an oblique transverse section, cross each other at right angles, whereas in the outer portion they are all parallel with one another, presenting, however, the peculiarity of not running straight on to the surface at right angles to it, but inclining towards the middle line of the skull.

In the genera *Sciurus*, *Pteromys*, *Tamias*, and *Spermophilus* the enamel rods, as seen in longitudinal section, start from the dentine at right angles to its surface ; in *Castor* they incline upwards at an angle of 60°, but preserve the distinction between the outer and inner layers very distinctly.

In the *Muridæ* the decussation of the layers in the inner part and their parallelism in the outer part of the enamel are also found, but, in addition to this, the borders of the individual prisms are slightly serrated, the serrations of contiguous rods interlocking.

In the porcupine sub-order (*Hystricomorpha*) the columns of the inner portion of the enamel pursue a serpentine course, nevertheless showing indications of a division into layers, becoming parallel in the outer portions as in other rodents. Small interspaces are found amongst the enamel rods of the porcupines.

In the hares (*Leporidæ*) the lamelliform arrangement and the division into outer and inner layers alike disappear.

The peculiarities in the disposition of the enamel fibres, which are so marked in the incisors, do not generally exist in the molars of the same species, except when these are of continuous growth.

Many minor differences in the arrangement of the enamel prisms exist, for a description of which the reader is referred to the original paper, but in general terms it may be said that the " enamel lamellæ have a different and distinctive character in each of the larger groups, and that the variety of structure is constant throughout the members of the same group. We may take, for example, the *Sciuridæ*, the *Muridæ*, and the *Hystricidæ*, in each of which the structure of the enamel is different, and in each is highly distinctive." And further the varieties in the structure of the dental tissue, so far as they are known, with a few isolated exceptions, justify and accord with the classification of the members of the order usually given.

It is stated by von Ebner that tubes exist in the enamel of hares and of *Cavia*, but that they do not communicate with the dentinal tubes. There is, however, no doubt that in the jerboa the tubes in the enamel are in continuity with those of the dentine.

The milk dentitions of the rodent have been investigated by a number of observers, with rather discrepant results. At all events, it may be said that the extent to which the milk teeth are developed varies much.

It has already been mentioned that in the hares and rabbits there are four incisors in the upper jaw, a small and apparently functionless pair being placed close behind the large rodent incisors ; but in very young specimens there are six incisors, of which the one pair are soon lost.

Professor Huxley (⁴) wrote : "The deciduous molars and the posterior deciduous upper incisors of the rabbit have been long known. But I have recently found that unborn rabbits possess, in addition, two anterior upper and two lower deciduous incisors. Both are simple conical teeth, the sacs of which are merely imbedded in the gum. The upper is not more than one-hundredth of an inch long, the lower rather larger. It would be interesting to examine fœtal guinea-pigs in relation to this point ; at present they are known to possess only the hindermost deciduous molars, so far agreeing with the marsupials." These additional teeth he rightly interpreted as being milk teeth, and not as representatives of an additional pair of incisors.

Huxley's observation has been confirmed by Pouchet and Chabry, Freund, Woodward, and others. The latter observer has reinvestigated the tooth development in the rabbit and finds (¹⁷) that

$\frac{\text{di.}_1}{\text{di.}_1}$ never cut the gum, and are absorbed in utero.

$\frac{\text{di.}_2}{0}$ is functional, and is shed about the third week after birth.

dpm $\frac{3}{2}$ are functional, and are shed about the same period as the last.

The squirrel also has milk incisors (Freund) ; three rudiments are described by that author, which Woodward, as it appears to the author with good reason, interprets as a milk incisor, as a vestigial milk incisor representing the second incisors of the hares and rabbits and as a third incisor (Freund regarding the last as a canine).

Woodward (*loc. cit.*) describes a pair of minute calcified rudiments in the mouse, though their presence is not quite constant. Thus the squirrel, the rabbit, and the mouse present three stages in the reduction of the vestigial milk incisors. To these Marett Tims (¹¹) adds a further stage in the guinea-pig (*Cavia*) in which a labial growth of the tooth band occurs, but no calcification has been observed. In other rodents no milk teeth are known in the front of the mouth.

Waterhouse (¹⁵) has found the milk molars still in place in the skull of a half-grown beaver ; while in the hares they are shed about the eighteenth day after birth, and in the guinea-pig disappear before birth.

Hares and rabbits have six milk molars in the upper and four in the lower jaw, which come into use, but differ from their successors in forming definite roots, and not growing from persistent pulps.

Milk premolars have been described in the hare and rabbits, in *Castor*, *Dasyprocta*, *Ctenodactylus*, *Hystrix*, *Atherura*, *Erethizon*, all porcupines, so that it is probable that further search will reveal traces of others. In *Atherura*, a brush-tailed porcupine, there is a single well-developed and functional milk premolar on each side of both jaws.

Other rodents, such as the rat, which has only three teeth of the molar series on each side, and the Australian water-rat (*Hydromys*), have no known milk teeth, and are hence perhaps truly monophyodont.

The change of teeth has been carefully investigated in the guinea-pig (*Cavia*) by Marett Tims (*loc. cit.*). It possesses as a functional dentition four cheek teeth on each side, which are generally regarded as

$$\mathrm{p}\,\frac{1}{1}\ \mathrm{m}\,\frac{3}{3}.$$

Cuvier had discovered that before birth in the molar region there was a single milk tooth. In the fœtal guinea-pig five cheek teeth are found in process of development. The deciduous tooth, Cuvier's milk molar, is the second, and the tooth which displaces it is not, as might have been expected, its morphological successor, but is the tooth which is developing in front of it and quite independently of it. This raises a doubt whether the deciduous tooth is a milk tooth at all. It appears as if it belonged to the same series as the functional teeth, in which case it must be regarded as a permanent tooth (probably the first of the molar series) which is shed before birth, and the guinea-pig would have no milk teeth at all. A somewhat similar doubt attaches to the single deciduous tooth of marsupials and other animals. (Cf. pp. 364 and 412.)

Rodents are fairly well represented in Eocene Tertiary deposits, but their ancestry is by no means clear. Cope considers that the Tillodontia (see p. 437) may have been the ancestors of existing rodents, and gives (²) an instructive series of reduction of certain incisors and hypertrophy of others in *Esthonyx, Psittacotherium, Calamodon*, and *Anchippodus*, in which one pair of very rodent-like incisors remain in the lower jaw. He holds with Ryder that continued severe use has resulted in hypertrophy of these teeth, and that the backward and forward excursions of the jaw have led to the disappearance of the postglenoid process in the articulation, allowing of the very posterior position of the lower jaw characteristic of rodents.

Forsyth Major (⁵) states that the investigation of early rodents lends no support to the tritubercular theory, but that a brachyodont bunodont molar is obviously the more primitive type among them, and that the more brachyodont the tooth the more it is multitubercular. He holds that in the molars of all mammals a tendency to reduction and simplification, which proceeds from the inner side outwards in the upper jaw and from the outer side inwards in the lower jaw, is traceable, and that the true tritubercular molar, having been arrived at in this way, is not a primitive, but a specialised type. (Cf. p. 344.)

Marett Tims finds that there is a reduction in the number of cusps on the molar teeth of *Cavia* during development, thus bringing embryological evidence in support of Forsyth Major's palæontological conclusions.

Tillodontia.

This order, comprising several genera, was proposed by Marsh to include some Wyoming fossil remains which, though not amongst the biggest, are "amongst the most remarkable yet discovered in American strata, and seem to combine characters of several distinct groups, viz., Carnivora, Ungulata, and Rodentia." In *Tillotherium* (Marsh), the type of the order, the skull has the same general form as in the bear, but in its structure resembles that of the Ungulata. Its molar teeth are of the ungulate type, the canines are small, and in each jaw there are a pair of large scalpriform incisors, faced with enamel, and growing from persistent pulps as in the rodents. The hinder pair of incisors are small and have not persistent pulps. It has been pointed out by Wortman that the greatly developed incisors are the second pair, and that the first and third are disappearing just as in the ancestors of the Proboscidea.

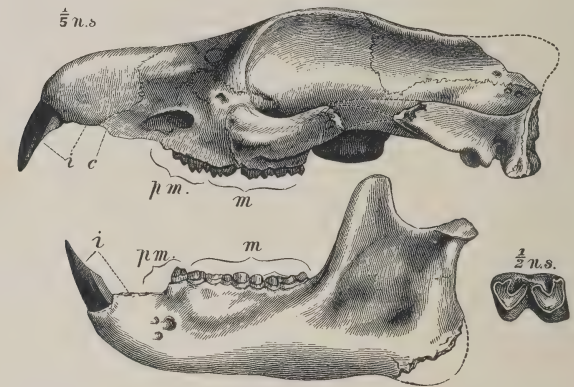

FIG. 270.—Upper and lower jaws of *Tillotherium* (Marsh).

Esthonyx (Cope), an Eocene mammal with a dentition roughly resembling that of a gigantic shrew, foreshadows this condition, having $i\frac{2}{3}$, of which $\frac{}{i_3}$ is extremely reduced, while $\frac{}{i_2}$ is enlarged, and its enamel confined to its anterior and external aspects; $\underline{i_1}$ is absent, $\underline{i_2}$ enlarged, with no enamel on its back, but none of these teeth grow from persistent pulps.

The adult dentition of *Tillotherium* is as follows:—

$$i\frac{2}{2}\ c\frac{1}{1}\ \text{prm}\ \frac{3}{2}\ m\frac{3}{3}.$$

"There are two distinct families: *Tillotheridæ* (perhaps identical with *Anchippodontidæ*), in which the large incisors grew from persistent pulps, while the molars had roots, and the *Stylinodontidiæ*, in which all the teeth have persistent pulps."

One genus (*Dryptodon*), known only by the lower jaw, had six teeth, described as "clearly incisors," the two inner pairs of which are small and cylindrical, the outer of enormous size, faced in front only with enamel, and with persistent pulps carried back under the premolars.

Whilst Flower endorses Marsh's view that Tillodonts have ungulate affinities and resemblances to rodents also, Cope, on the other hand, regarded the Tillodonts as being the ancestors of the rodents. This is disputed by Dr. Wortman (18), who says that he fails to discover any traces of ungulate relationship, and he prefers to refer them to those generalised forms with insectivorous affinities which Cope groups as Bunotheria. The adaptive character of incisors faced with enamel and of persistent growth he would appear to consider as not going far towards establishing more than a superficial resemblance to the Rodentia. He holds that Tillodonts are probably descendants of Esthonyx, itself allied to the shrews, and that they may also have given origin to the Toxodonts.

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CHAPTER XVIII.

THE TEETH OF CETACEA, UNGULATA, AMBLYPODA AND CONDYLARTHRA.

Cetacea	Odontoceti	*Physeteridæ.*
		Platanistidæ.
		Delphinapteridæ.
		Delphinidæ.
	Mystacoceti	*Balænidæ.*
		Rhachianectidæ.
		Balænopteridæ.

THIS order is divided into two groups, namely, the toothed whales, or Odontoceti, and the whalebone whales, or Mystacoceti; these two groups are sharply defined from one another.

No cetacean is known to develop more than one set of functional teeth, and these, when present in any considerable numbers, closely resemble one another in form. The teeth, however, of the extinct *Zeuglodon* and *Squalodon*, which have about 361 teeth, are heterodont in character.

Squalodon had about sixty teeth. The four front teeth on each side were simple in form, the next four nearly simple, whilst the last seven had sharp cuspidate edges, and were implanted by two roots.

Kükenthal has shown that, at all events in *Beluga*, *Tarsiops* and *Globiocephalus*, rudiments of successional teeth are to be found to the inner sides of the functional teeth, which latter are thus shown to be persistent milk teeth, though Leche considers it still an open question. [The conditions as to the number and relations of the dentitions present in the developing jaw are similar to those found in the marsupials. In both cases there is much to justify the view that the functional teeth belong to the successional or replacing series of the mammalia generally (p. 328).]

The Cetacea appear to have descended from an ancient heterodont diphyodont stock, probably with ungulate affinities, and to have reverted to a primitive homodont series, represented by a single dentition.

In *Phocæna* (common porpoise) the enamel-organs are not much differentiated, the internal epithelium cells remaining rounded, but in *Balænoptera* the differentiation goes further, although the teeth are never to be cut.

The teeth of Cetacea are usually composed of hard dentine, with an investment of cementum. After the attainment of the full dimensions of the teeth what remains of the pulp is very commonly converted into secondary dentine; tips, and even entire investments of enamel, are met with in many of the order. The dentine is remarkable for the very numerous interglobular spaces which it contains; these are clustered in concentric rows, so as to give rise to the appearance of contour lines. The cement is often of great thickness, and the lacunæ in it are abundant; its lamination is also very distinct.

The **Dolphin** (*Delphinus*) may be taken as representing a generalised cetacean dentition. In it the teeth are very numerous, there being about 200; they are slender, conical, slightly curved inwards, and sharply pointed. As they interdigitate with one another, there is very little wear upon the points, which consequently remain quite sharp. The largest teeth are those situated about the middle of the dental series.

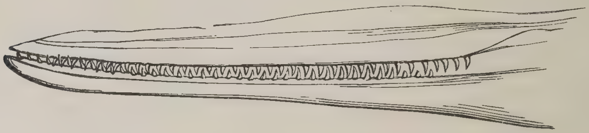

Fig. 271.—Jaws of common dolphin (*Delphinus*).

Many variations in the number and form of the teeth are met with. The porpoise (*Phocæna*) has not more than half the number of teeth possessed by the dolphin. They are small, and have compressed crowns with cylindrical, contracted necks. In *Inia*, a fresh-water form akin to the dolphins, the posterior teeth have a distinct tubercle on the inner side. The extent to which sockets, seldom very complete, are developed also varies greatly in the Cetacea, in some there being little more than a continuous groove, in which the teeth are implanted. There is a little confusion in the nomenclature, the popular names porpoise, dolphin, and grampus being applied somewhat vaguely to several different genera. Thus the grampus of sailors is the genus *Orca* of naturalists. The genus *Grampus* of naturalists is a quite distinct creature, with few teeth, only three to seven on each side, and these only in the lower jaw, and is furnished with fewer teeth than the dolphin or the porpoise, but they are very

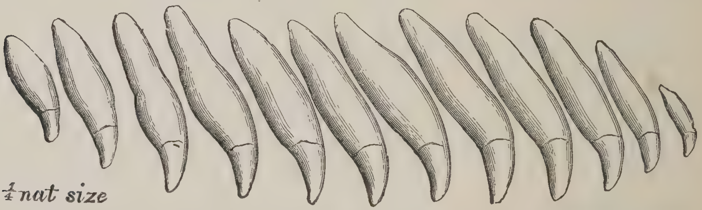

Fig. 272.—Teeth of upper jaw of a grampus (*Orca*). (After Professor Flower.)

large and stout, and exist in both jaws. The teeth of the grampus (*Orca*) become worn down on their opposed surfaces, and coincidently with their wearing away the pulps become calcified. In the Oxford Museum there is a grampus in which, owing to a distortion of the lower jaw, the teeth, instead of interdigitating, became exactly opposed to one another; the consequence of this was that the rate of wear was greatly increased, and the pulp cavities were opened before the obliteration of the pulp by calcification had taken place,* so that the pulps died and abscesses around the teeth had resulted.

These animals are strong and fierce; they attain to a length of 20 feet, feeding on fish, seals, and other cetaceans smaller than themselves, and combining in numbers to attack even whales, which they thus succeed in killing.

It occasionally happens in the *Delphinidæ* that small additional teeth are interposed between the regular alternating teeth.

The remaining toothed cetaceans which will be noticed all present some reduction from the dentitions thus far alluded to. Thus *Beluga*, the white whale, has from eight to ten teeth on each side of each jaw, but they are rather small, and are confined to the anterior half of the jaws.

The **Sperm Whale** (*Physeter*) grows to a gigantic size, 50 to 60 feet in length, and is pursued for the sake of its blubber, which yields sperm oil, and for the oil contained in the cells of its head (spermaceti). It feeds on large and even gigantic cuttle-fish, and upon fish, which as a rule it swallows whole without biting them, as might be expected from its inefficient dental armament.

The teeth are numerous in the lower jaw, but in the upper jaw there are only a few curved, stunted teeth, which remain buried in the dense gum, and are generally lost from skulls. Ritchie and Edwards have, however, recently noted the occurrence of functional teeth in the upper jaw and in more than one specimen (^{8}). The teeth of the lower jaw are retained in shallow and wide depressions of the bone by a dense ligamentous gum, which, when stripped away, carries the teeth with it. Thus every intermediate stage between this slight implantation and the well-developed stout sockets of the grampus is met with in the Cetacea.

In tertiary deposits in Patagonia a small sperm whale has been found with a full series of enamelled teeth in the upper jaw.

In the **Bottle-nosed Whale** (*Hyperoödon bidens*) the only large teeth present are two (sometimes four) conical, enamel-tipped teeth, which remain more or less completely embedded within the gum, near to the front of the lower jaw. In addition to these there are 12 or 13 very small rudimentary teeth loose in the gums of both jaws (Eschricht, Lacépède).

The **Ziphoid Cetaceans** present one of the most curious and inexplicable dentitions to be found in any animal. The upper jaws are edentulous, as in the Hyperoödon, and the lower jaws contain only a single tooth upon each side; but these teeth have attained to great proportions, measuring in full-grown specimens as much as 10 inches in length; they are thin, flat and strap-shaped, straight for some considerable part of their length and then curving over towards each other, may even cross each other above the upper jaw, so that they actually limit, to a considerable extent, the degree to which the jaws can be opened.

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* "Trans. Odontol. Society," 1873. When this paper was published the author was not aware that Eschricht had previously published a similar observation.

A few small additional teeth are often found in ziphoid cetaceans, but these are generally lost from skulls.

It is not merely difficult to see of what use these teeth can be, but it is hard to suppose that they can be otherwise than actually detrimental to their possessors in the pursuit of food. There is some reason to suppose that the presence of well-developed tusks is a character of the male sex, though upon this point the evidence is not quite complete. Females have been found with their skins curiously scored in two parallel lines, especially near the pudenda, suggesting the idea that they are liable to be attacked by the males.

The structure of these teeth is not less peculiar than their general form. The summit of the tooth, which starts off nearly at right angles to the shaft (and so, the shaft being curved over the top of the upper jaw, comes to stand nearly vertically), consists of a denticle bluntly pointed and made up of dentine coated with enamel. This denticle of triangular shape is only about a third of an inch in length, and in the adult specimen described by Professor Sir William Turner had the enamel coat partially worn off.

In the *Challenger* Reports ("Zoology," vol. i.) he says: "In the earlier stage their structure does not differ materially from the ordinary type of tooth one meets with, say, in the human or carnivorous jaw, the crown being formed by enamel, the fang by cement, whilst the great body of the tooth consists of dentine, in which is a marked pulp cavity, communicating with the exterior by a slit-like aperture at the root of the fang. The exceptional character these teeth exhibit in the erupted condition is due to the disappearance of the enamel from the crown, to the cessation in the development of the ordinary dentine, to the excessive formation of osteo-dentine, of modified vaso-dentine, and of cement, by means of which the pulp cavity becomes almost obliterated, and the fang assumes dimensions which, in the case of *Mesoplodon layardii*, lead to the production of a tooth having the very remarkable form and relation to the beak which I have described."

As may be gathered from the above, the development of the tooth begins by the formation of the denticle, which is of an ordinary structure; the enamel, however, soon ceases to be formed, and, but very little further down, the true dentine also, not, however, before cementum has begun to be formed upon its exterior. (See *c* in Fig. 273.) Then there comes an abrupt change in direction, and in the place of true dentine we find a coarser textured tissue which contains large vascular canals.

This Sir W. Turner and Sir E. Ray Lankester regard as a vaso-dentine, seeing that it is in all probability a product of the dentine pulp. Of this the great mass of the tooth consists, but it has throughout its length an investment of cementum of an ordinary type, which forms a complete external layer, laminated, full of lacunæ and for the most part devoid of Haversian canals.

Immediately beneath this layer there is, if the distinction be not exaggerated in the drawing, a definite stratum of tissue of material thickness which is characterised by an abundance of vascular canals arranged perpendicularly to the surface (*a* in Fig. 273), which is regarded by Sir William Turner as belonging to the dentine group of tissues, *i.e.*, as being a vaso-dentine. But there is a difficulty in accepting this view, viz., that near to the denticle it is seen to lie distinctly outside the true fine-tubed dentine (see Fig. 273), which it overlaps to a considerable extent. Now if this tissue was formed by the dentine pulp we should have the anomaly of a pulp first forming a very vascular vaso-dentine, then changing to form a fine-tubed normal dentine (which is exactly the reverse of what is met with in other creatures in which the pulp forms these two structures), and finally reverting to the building up of a vaso-dentine.

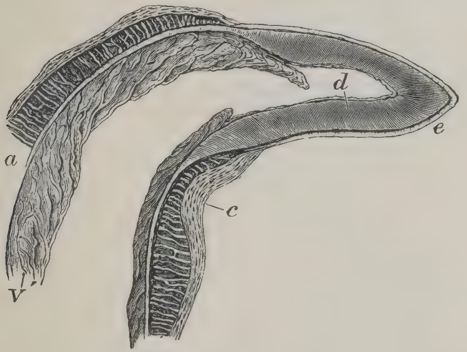

Fig. 273.—Upper part of tooth of *Mesoplodon*. (After Professor Sir W. Turner.) *a*. Tissue of doubtful origin, permeated by vascular canals. *c*. Cementum. *d*. Dentine. *e*. Enamel. *v*. Vaso-dentine.

Judging by analogy, this seems so improbable that, in the absence of more positive knowledge and simply judging from the figure, one would be inclined to refer this layer to the cementum. Lower down in the shaft of the tooth anastomoses take place between the tubes of this layer and those of the unquestionable pulp products, but anastomoses between dentine tubes and enamel tubes and between dentine tubes and cement lacunæ are of common occurrence in many animals, so that this communication does not prove anything as to their respective origin.

However, Sir Ray Lankester lays stress upon the globular botryoidal structure of this layer, which he states shades off into the fine-tubed dentine, so that it may perhaps be regarded as an excessive development of the globular layer of dentine rather than as a vaso-dentine. In reconciliation of the discrepancy between the two descriptions, it is suggested by Turner that the vascular canals seen by him in this layer may have become obliterated in the presumably much older specimen described by Lankester.

The central pulp cavity becomes reduced to the merest traces, so that the completed tooth is almost solid.

In the **Narwal** (*Monodon monoceros*) two teeth alone persist, and these are in the upper jaw. In the female the dental germs become calcified, and attain to a length of about eight inches, but they remain enclosed within the substance of the bone, and their pulp cavities speedily fill up. In the male one tusk (in some very rare instances both) continues to grow from a persistent pulp till it attains to a length of ten or twelve feet, and a diameter of three or four inches at its base. This tusk (the left) is quite straight, but is marked by spiral grooves, winding from right to left. It is curious that in one of the specimens, in which the two tusks had attained to equal and considerable length, the spirals on the two wound in the same direction ; that is to say, as regards the sides of the head, the spirals were not symmetrical with one another.

The tusk of the male narwal may fairly be assumed to serve as a sexual weapon, but little is known of the habits of the animal.

Professor Sir William Turner has noted the occurrence of two stunted incisor rudiments in a fœtal narwal : these obviously represent a second pair of incisors, and attain to a length of half an inch, but are irregular in form ; they are situated a little behind the pair of teeth which attain to more considerable dimensions. All trace of this second pair of incisors is lost in adult skulls.

Mystacoceti.—The remaining group of cetaceans, the *Mystacoceti*, or whalebone whales, are characterised by being, in the adult condition, destitute of teeth, but prior to birth the margins of both upper and lower jaws are covered with a series of nearly globular rudimentary teeth which become calcified, but are speedily shed, or rather absorbed.

The fœtal teeth of the *Balænoptera rostrata* (the **Rorqual,** perhaps the commonest of the whalebone whales, which is sometimes stranded on British coasts, and has short and inferior whalebone) have been carefully described by M. Julin (^{2}), the *Balænopteridæ* having been previously supposed to be without rudimentary teeth. The ramus contained forty-one tooth-germs, each furnished with an enamel-organ and dentine bulb, with a slight capsule ; these were lodged in a continuous groove in the bone above the vessels, thus recalling the condition of the parts in a human embryo at a certain stage. A very small amount of calcification takes place, a mere film of dentine being formed upon the dentine bulb. But what is very remarkable is that the dentine bulbs are simple near the front, bifid in the middle, and trifid at the back of the mouth; in other words, these tooth germs would go to form heterodont teeth, not unlike those of some seals, or of *Squalodon*. Hence it has been suggested that the whale may be descended from some such ancestral form.

Kükenthal states that as these trifid teeth become absorbed they may separate into three. Moreover, he states that there are traces of successional rudiments.

From the upper jaw of an adult whalebone whale there hang down a series of plates of baleen, placed transversely to the axis of the mouth, but not exactly at right angles to it. The principal plates do not extend across the whole width of the palate, but its median portion is occupied by subsidiary smaller plates. The whalebone plates are frayed out at their edges and collectively form a concave roof to the mouth, against which the large tongue fits, so as to sweep from the fringes whatever they may have entangled. The whale in feeding takes in enormous mouthfuls of water containing small marine mollusca; this is strained through the baleen plates, which

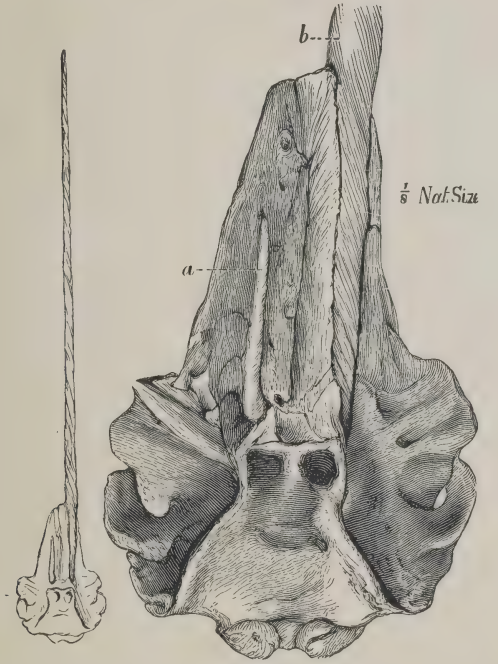

FIG. 274.—Cranium of narwal (*Monodon monoceros*). *a*. Stunted tooth, with its basal pulp cavity obliterated. *b*. Long tusk. The small figure, giving the whole length of the tusk, shows the proportion which it bears to the rest of the skull.

retain the Pteropods and other small creatures, while the water is expelled. Then the tongue sweeps the entangled food from the fringe of the baleen plates, and it is swallowed.

When the mouth is closed the baleen plates slope backwards towards the throat, but when it is opened by their elasticity they spring downwards to a vertical position, so as to still fill up the mouth, and as the mouth closes and expels the water, they act as strainers.

Each plate consists of two dense, but rather brittle, laminæ, which enclose between them a tissue composed of bodies analogous to coarse hairs. By the process of wear the brittle laminæ break away, leaving projecting from the edge the more elastic central tissue in the form of stiff hairs.

Each plate is developed from a vascular persistent pulp, which sends out an immense number of exceedingly long thread-like processes, which penetrate far into the hard substance of the plate. Each hair-like fibre has within its base a vascular filament or papilla; in fact, each fibre is nothing more than an accumulation of epidermic cells, concentrically arranged around a vascular papilla, the latter being enormously elongated. The baleen plate is composed mainly of these fibres, which constitute the hairs of its frayed-out edge, but in addition to this there are layers of flat cells binding the whole together, and constituting the outer or lamellar portion. As has been pointed out by Professor Sir William Turner (10), the whalebone matrix having been produced by the cornification of the epithelial coverings of its various groups of papillæ, is an epithelial or epiblastic structure, and morphologically corresponds not with the dentine, but with the enamel of a tooth.

The whole whalebone plate and the vascular ridges and papillæ which form it may be compared to the strong ridges upon the palates of certain Herbivora,* an analogy which is strengthened by the study of the mouth of young whales prior to the cornification of the whalebone.

It must not be supposed that because in the dolphins, &c., there is a simple homodont dentition, they are in any way the parent form of other mammalia. On the contrary, the possession of some amount of hair on the skin, the nature of the rudimentary teeth and many other characters, point to their being extreme, and in some particulars degenerated modifications of other, and probably terrestrial, mammals, and Kükenthal goes so far as to give the opinion that the two groups, the toothed whales and the whalebone whales, have had a distinct origin.

Thus, like the Edentata, the Cetacea have become homodont and practically monophyodont by a retrograde process, and the superficial resemblance of their simple conical teeth to those of a reptile is misleading.

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* Doubt has been thrown on this by some recent writers.—H. W. M. T

Teeth of the Ungulata.

UNGULATA	ARTIODACTYLA	Non-ruminantia Suoidea	*Hippopotamidæ.* *Suidæ.*
		Tylopoda	*Camelidæ.*
		Pecora	*Cervidæ.* *Bovidæ.* *Giraffidæ.*
		Traguloidea	*Tragulidæ.*
	Perissodactyla		*Tapiridæ.* *Rhinocerotidæ.* *Equidæ.*

This is a group of animals of which a vast number of forms are extinct, and are only imperfectly known. Recent discoveries, especially those of Marsh, Cope, Osborn, Wortman, and many others, in the rich deposits of America have brought to light a very large number of strange and highly interesting forms, which, while they have not done away with the old division of Ungulata, or hoofed mammals, into the artiodactyle (even-toed) and perissodactyle (odd-toed) ungulates, have brought within it, to a certain extent, Hyracoidea and Proboscidea, and have introduced a number of existing forms which will not fit into either of the old divisions.

Provisionally, they may be grouped into Ungulata Vera and Subungulata.

The Ungulata Vera comprise—

(i.) Artiodactyles, or even-toed Ungulata	Hippopotamus, Pigs, Anoplotherium, Cows, Sheep, Deer, and other Ruminants.
(ii.) Perissodactyles, or Ungulata with an odd number of toes	Horses, Tapirs, Rhinoceros, Palæotherium.

The distinction between the two groups is strongly marked, if living animals alone be considered; but, as Huxley pointed out, increasing knowledge of fossil forms has partly broken down the line of demarcation.

The ill-defined group of—

(iii.) Subungulata, or Ungulata Polydactyla, comprising	Hyracoidea, Proboscidea, Amblypoda, Toxodontia, Tillodontia, &c.

But fortunately it is not necessary in an elementary work on odontology to do more than present the descriptions of the several creatures somewhere near their right places, and so the difficulties of the classification of the Ungulata need not be discussed.

Of Eocene Ungulata it may be said that almost all possessed the full mammalian dentition, *i.e.*,

$$\text{i}\,\frac{3}{3}\ \text{c}\,\frac{1}{1}\ \text{pm}\,\frac{4}{4}\ \text{m}\,\frac{3}{3} = 44,$$

and a few had a larger number.

A great many of them had five toes, and were otherwise less specialised than modern forms.

Moreover, as we look at the patterns of the molar teeth, we find them far more simple, trituberculate or quadrituberculate crowns being the rule.

In the earlier forms the molars were short and distinctly rooted (*brachyodont*). Those with much longer crowns, such as the horse, are termed *hypsodont*, and occur later. When the surfaces of the molars present blunt cones, they are termed *bunodont*, and when they are lengthened out antero-posteriorly and curved, they are called *selenodont*, *e.g.*, as in the sheep.

In the more generalised types, such as, amongst recent ungulates, pigs and tapirs, for example, the cheek teeth have low cusps, so that in all stages of wear the bottom of the intervening valleys is in view; but in the long-crowned teeth of ruminants and the still longer ones of the horse the bottom of the valleys (in the latter case filled in with cementum) cannot be seen at all until the teeth are worn down.

In all existing ungulates the quadrituberculate type of tooth has been reached, but amongst the earlier ones the trituberculate pattern still persisted, or at all events persisted in their immediate ancestry, if such forms as *Phenacodus* be regarded as the parent forms of ungulates.

The modern Ungulata are all fitted for a vegetable diet, though possibly a few forms may occasionally prey upon much weaker animals. Indeed, among the extinct Ungulata there are some which tend to bridge the gap between existing Ungulata and Carnivora, wide though it now is.

There is a tendency to the reduction of teeth in the front of the mouth, to the suppression of canines, and to a great development of cheek teeth, in relation to their vegetable diet. The milk dentition is generally well developed, and in the case of modern domesticated animals remains in use for a considerable time.

In size they range from the little extinct artiodactyle *Hypsodon* described by Matthew, which was no larger than a rabbit, to the huge *Amblypoda*. It may save recapitulation to give at this point some account of the evolution of ungulate molars.

The complicated-looking patterns found in the cheek teeth of ungulates have long been studied with no little care, as it has been found that they are a guide to affinity, but unfortunately different writers have made use of very different terminologies in describing these teeth. Whether the tritubercular theory be adopted or not, its advocates, and notably Osborn, have had access to a great number of extinct forms till recently unknown, and have been able to determine the homologies of the various cusps and ridges in a manner previously impossible. Hence the terminology adopted by them is to be preferred to any of the older designations. The termination *-cone* is employed for the principal or crown cusps, and its diminutive *-conule* for smaller intermediate cusps. With the exception of the hypocone, which, although derived from the cingulum, was very early established as a crown cusp, all peripheral cusps, derived from elevations of the cingulum or borders of the crowns, are called styles.

The crests which are such conspicuous features in ungulate teeth prior to any wear taking place are always built up of two or more cusps and styles, and are denoted by the termination *-loph ;* and in

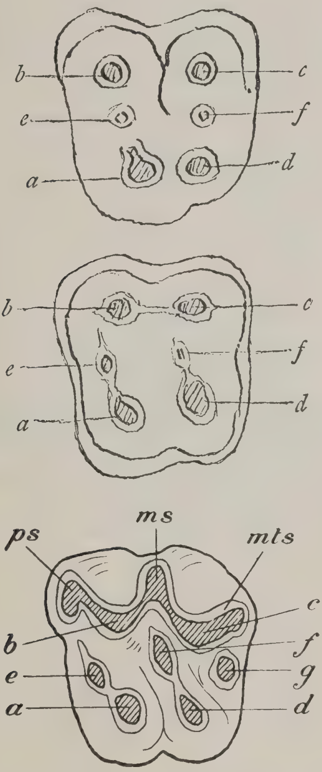

Fig. 275.—Description of figure. (After Osborn, "Studies Biol. Lab. Columbia College," "Zoology," vol. i., No. 2.) Teeth of *Euprotogonia*, *Hyracotherium*, and *Anchitherium*. *a.* Protocone. *b.* Paracone. *c.* Metacone. *d.* Hypocone. *e.* Protoconule. *f.* Metaconule. According to Osborn's later nomenclature in *Anchitherium*, *a* and *e* = protoloph ; *d* and *f*, metaloph ; the whole ridge *b* to *c*, ectoloph ; *ps*, parastyle ; *ms*, mesostyle ; *mts*, metastyle.

all cases the termination *-id* denotes the corresponding part of the lower teeth. To give an example of the application of these terms, the tooth of a rhinoceros is truly lophodont, since all its cusps have lost their integrity, and are fused into *-lophs*. In general terms, whilst the trigon and talon serve in earlier mammals and in Carnivora to distinguish between the cutting and the crushing portions of the crown, in ungulates the trigon is lowered to the same level as the talon, and loses its apparent distinction from it. At first the cusps remained distinct (bunodont type, which still persists in many, *e.g.*, the pigs), but gradually there came in the lophodont and selenodont forms, in which the cusps lost their integrity by being joined into ridges, which ridges again became curved or sinuous, and accessory styles being added still further increased the complexity of pattern. In what Schlosser terms the modernisation of the type he considers the obliquity of the ridges to be a survival of the obliquity of the sides of the primitive triangles. And, finally, the superadded "styles" attain to a size and importance equal to the earlier cusps, and when they too become fused into ridges or *lophs* create a complexity which it would have been impossible to unravel without the help of the earlier transitional forms.

It will be gathered that the chief importance in the comparison of various forms lies in the identification of the cusps and ridges, but as one often has to deal with a tooth in which the top is worn more or less level, it is desirable to have a name for the areas which intervene, and which are filled up with cementum. For these Cuvier's term *fossettes* is retained.

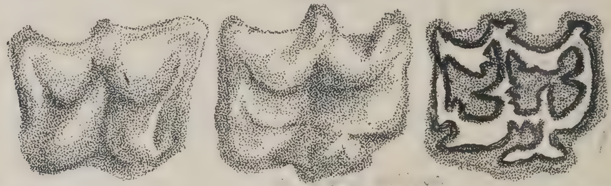

Fig. 276.—Grinding surfaces of an unworn tooth of *Anchitherium*, of unworn tooth of horse, and of worn tooth of horse. In the latter the light areas are dentine, the shaded areas cementum, and the black border between them enamel. (After Flower and Lydekker.)

The foregoing illustration (Fig. 275), adapted from Osborn, will serve to show, in some measure, the stages by which such transformations of pattern are brought about.

In the first the bunodont tooth, with its four principal cusps and near to the middle of its crown the subsidiary cusps, is seen to be tending towards a lophodont type by the joining of these with the protocone and hypocone.

In *Hyracotherium* this has gone further: the outer cusps are joined by a ridge (longitudinal), and the protocone and protoconule and the hypocone and metaconule are joined by ridges (transverse, or rather oblique, to the line of the alveolus), the *protoloph* and the *metaloph*, whilst the external cusps, the paracone and metacone, are merged in a continuous ridge, the *ectoloph*, fortified at three points by cingulum cusps or styles. At this stage the tooth is not far from that of the *Tapir*, or from that of *Rhinoceros*.

In the third figure and also in Fig. 276 is seen the tooth of *Anchitherium*, one of the ancestors of the horse.

In this all the ridges are more developed, so that the identity of the cusps is nearly lost; the external ridge has become sinuous, and pillars have been added, conspicuously at its left hand end and less so at its right, while an additional detached pillar appears to the right.

By further increase in the obliquity and curvature of the ridges, and by the appearance of other detached pillars, the tooth pattern becomes transformed into that of *Hipparion*, in which two pillars on the inner side remain distinct, and into that of the horse, in which they become more or less fused with the curved ridges.

The outer ridge or wall is in the upper molar of the horse doubly bent, the concavities looking outwards. The transverse ridges start inwards from its anterior end and from its middle, and they curve backwards as they go, to such an extent as to include crescentic spaces between themselves and the outer wall. To this must be added a vertical pillar which is slightly connected with the posterior end of each crescentic edge (these pillars are in *Hipparion* quite detached), and a second which is fused with the other crescent.

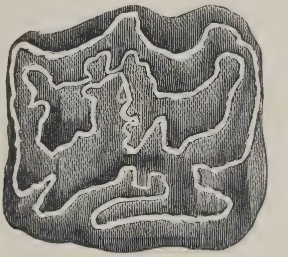

Fig. 277.—Upper molar of horse.

The lower molars of the horse present the double crescent, just like those of the rhinoceros, save that vertical pillars are attached to the posterior end of each crescent, thus slightly complicating the pattern of the worn surface. The interspaces of the ridges and pillar are in the horse solidly filled in with cementum. The extinct ancestors of the horse are now, however, pretty well known (5). *Hyracotherium*, found in the Lower Eocene, is probably the most primitive stage known. It was no larger than a cat, and had four toes on each forefoot and three on each hindfoot; a single splint bone represents one missing digit on each foot. The teeth carried rounded cusps just beginning to show indications of fusion into crests. Then came *Eohippus*, the size of a fox, and in most respects very like *Hyracotherium*, except that the cusps of the molars show more indication of fusion to form crests; it had four well-developed toes and a rudiment of the fifth (forefoot). Next came the Eocene *Orohippus* (four-toed); the Miocene *Mesohippus*, as large as a sheep (three-toed, with rudimentary splint); the Upper Miocene *Miohippus* (three-toed); the Lower Pliocene *Protohippus*, as large as an ass (three-toed, but only the middle one reaching the ground), which was like the European *Hipparion;* then the Pliocene *Pliohippus*, which has lost the small hooflets, whilst in the Upper Pliocene the true *Equus* first appears.

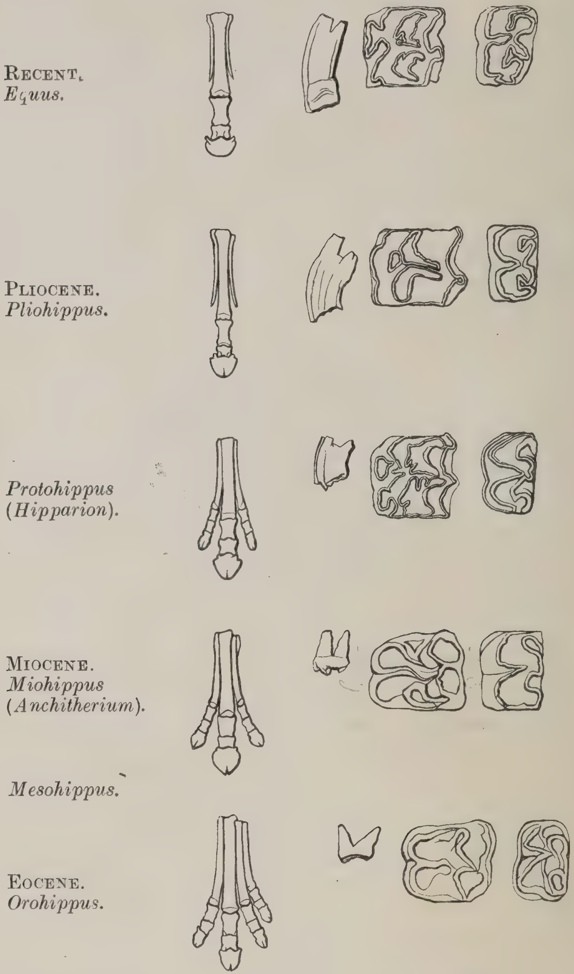
RECENT.
Equus.
PLIOCENE.
Pliohippus.
Protohippus
(*Hipparion*).
MIOCENE.
Miohippus
(*Anchitherium*).
Mesohippus.
EOCENE.
Orohippus.

FIG. 278.—Ancestry of the horse. (After Marsh.)
The forefoot and surfaces of upper and lower molars.

Eohippus had forty-four teeth, the molars being quite distinct from the premolars, with short crowns and roots *; in *Orohippus* the last premolar is like the true molars, while in *Mesohippus* two premolars are like the true molars.

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* Ancient deer also had short crowns to their molar teeth.

Coincidentally with the elaboration of the crown pattern a great lengthening of the crown took place, so that there was much more material available for wear, but considerable crown elaboration had arisen before the teeth ceased to be brachyodont.

The great lengthening which has taken place in the hypsodont molars of the horse since the time of the Miocene *Miohippus* (*Anchitherium*) is well seen in Fig. 279.

It is perfectly obvious that the hypsodont type of tooth provides for a much longer period of severe attrition before the roots are formed than the brachyodont tooth of *Miohippus*, so that it is probable that the food of the modern horse is of a drier and harsher kind than that of its ancestors. Indeed, the small early ancestors seem to have been adapted to a forest life, whereas the modern horse inhabits level grass plains, often rather dried up, and its food needs more mastication.

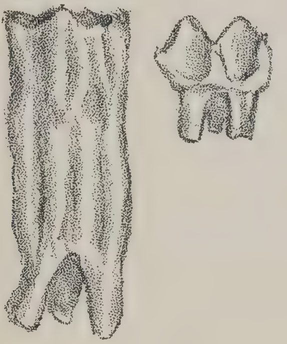

FIG. 279.—Outer view of second upper molar of *Anchitherium* (brachyodont) and of horse (hypsodont).

In *Miohippus* the surface had two nearly transverse and slightly curved ridges with valleys between them, but the valleys were shallow and were not filled up with cementum.

As the crowns of the teeth became longer, and the valleys between the cusps very much deeper, they became filled up solidly with cementum, which not only added strength, but as the tooth wore down, preserved a rough surface by affording three tissues of different hardness; for as the tips of the cusps wore down the enamel was worn off, and areas of dentine surrounded by a rim of enamel became exposed, and the intervening cementum also came into wear, the efficiency of the surface for grinding purposes being yet further increased by the sinuosity of the enamel rings.

The Teeth of Artiodactyle Ungulates.

Artiodactyle, or even-toed, ungulates comprise, amongst living animals, pigs, Hippopotami, camels, sheep, oxen, &c.

They are grouped into

(i.) Bunodonts, or Suina, comprising pigs and Hippopotami.
(ii.) Selenodonts, comprising *Anoplotheridæ* and the ruminants.
  (a.) The Tylopoda, or camels.
  (b.) Pecora, or sheep, oxen, and deer.
  (c.) The Traguloidea (chevrotains), small deer of S. Asia, which are somewhat intermediate between the Suidæ and the deer.

The primitive Artiodactyla all had forty-four teeth of brachyodont type; in later geological times they became long-toothed (hypsodont), like recent sheep and oxen. The premolars differ markedly both in size and pattern from the true molars.

Of those artiodactyle ungulates which are not ruminants the common **Pig** may be taken as an example.

The dental formula is $i\frac{3}{3}\ c\frac{1}{1}\ p\frac{3}{3}\ m\frac{3}{3}$, or perhaps $p\frac{4}{4}\ m\frac{3}{3}$.

The position of the upper incisors is peculiar, the two first upper incisors, separated at their bases, being inclined towards one another so that their apices are in contact; the third pair are widely separated from the inner two pairs of incisors. The lower incisors are straight, and are implanted in an almost horizontal position; in both upper and lower jaws the third or outermost incisors are much smaller than the others.

The lower incisors are peculiar in having upon their upper surfaces a strongly pronounced sharp longitudinal ridge of enamel, which gets obliterated by wear.

An interval separates the incisors from the canines, which latter are very much larger in the male than in the female, and in the wild boar than in the domesticated animal. Castration arrests the further development of the tusks; and the peculiarities as to size and direction which characterise the tusks of the adult animal are not represented in the canines of the milk dentition.

The form and direction of the canines are alike peculiar. The upper canine, which in its curvature describes more than a semicircle, leaves its socket in a nearly horizontal direction, with an inclination forwards and outwards. After rounding past the upper lip its terminal point is directed upwards and inwards. The enamel upon the lower surface of the tusk is deeply ribbed; it does not uniformly cover the tooth, but is disposed in three bands. The lower canines are more slender, of much greater length, and by wear become more sharply pointed than the upper ones; they pass in front of the latter, and the worn faces of the two correspond.

The lower canine is in section triangular, one edge being directed forwards, and its sides being nearly flat. Enamel is confined to the internal and external anterior surfaces ; the posterior surface, which plays against the upper canine, is devoid of enamel, and the tooth is kept constantly pointed by the obliquity with which its posterior surface is worn away. The tusks of a boar are most formidable weapons, and are capable of disembowelling a dog at a single stroke, but they are greatly exceeded by those of the African wart-hog (*Phacochœrus*), which attain to an immense size, and are articles of commerce, being used for small articles as a substitute for ivory.

In the domestic races the tusks of the boars are much smaller than in the wild animal, and it is a curious fact that in domestic races which have again become wild the tusks of the boars increase in size at the same time that the bristles become more strongly pronounced. Darwin suggested that the renewed growth of the teeth may perhaps be accounted for on the principle of correlation of growth, external agencies acting upon the skin, and so indirectly influencing the teeth.

As in most artiodactyles, the teeth of the molar series increase in size from before backwards ; thus the first premolar (? milk molar) has a simple wedge-shaped crown, and two roots ; the second and third by transitional characters lead to the fourth premolar, which has a broad crown with two principal cusps, and has four roots.

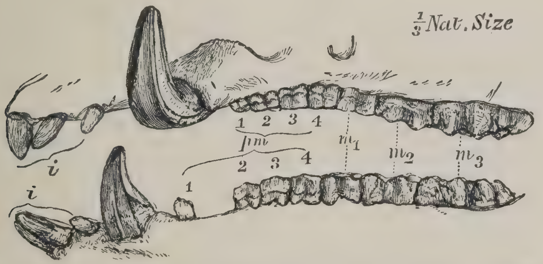

FIG. 280.—Upper and lower teeth of wild boar (*Sus scrofa*). In this specimen the tusks are not so largely developed as they sometimes may be seen to be.

The first premolar is a tooth about which there is a doubt whether it is a retained milk tooth or a permanent tooth which has not had a predecessor.

Of this tooth Lesbre (3) says that it is cut about the fifth month, after the milk molar, but before the replacing teeth. As there is no vertical succession in the case of this tooth, he regards it as a milk tooth which was delayed and dwarfed by the development of the great canine close to and below it. As a proof, he says that he has discovered in one case a successional tooth beneath it. The premolars of the pig are cut in order from behind forwards, pm_4 being erupted first.

The dental formula of persistent or more or less persistent teeth would then read

$$i\,\frac{3}{3}\ c\,\frac{1}{1}\ dm\,\frac{1}{1}\ pm\,\frac{3}{3}\ m\,\frac{3}{3}.$$

Nawroth, as quoted by Marett Tims, says also that this tooth is occasionally replaced in the pig, so that as a general rule we may say the young pig has d.m. $\frac{4}{4}$, of which the first remains in place till the permanent dentition is nearly complete and then falls out without having any successor.*

The first true molar has four cusps divided from one another by a crucial depression; and the cingulum in front, and yet more markedly at the back, is elevated into transverse ridges. In the second molar the transverse ridge is more strongly developed, and the four cusps are themselves somewhat divided up into smaller accessory tubercles.

The last molar measures, from front to back, nearly twice as much as the second; and this great increase in size is referable to a great development of the part corresponding to the posterior ridge or cingulum of the second molar, which has become transformed into a great many subsidiary tubercles.

That such is a correct interpretation of its nature is indicated by our being able to trace the four principal cusps, though modified and not divided off, in the front part of the tooth, of which, however, they do not constitute more than a small part. Those ungulates in which the surfaces of the molar teeth are covered by rounded or conical cusps are termed "bunodonts," in contradistinction to those which present crescentic ridges on the masticating surface of their molars, and which go by the name of "selenodonts."

In the **Wart-hog** (*Phacochœrus*), the genus with very large canines, the disproportion between the last true molar and the other teeth is yet more striking.

In antero-posterior extent the third molar equals the third and fourth premolars and the first and second true molars (the whole number of other teeth of the molar series possessed by the animal) together.

When a little worn its surface presents about thirty islands of dentine, surrounded by rings of enamel, the interspaces and the exterior of the whole being occupied by cementum. Of course, prior to the commencement of wear, each of these islands was an enamel-coated cusp.

The wart-hog's dentition has, however, another instructive peculiarity: the first true molar is in place early, and becomes much worn down (this is true, in a less degree, of the common pig, and indeed of most Ungulata). Eventually it is actually shed; the same fate later befalls the third premolar and second true molar, so that the dentition in an aged specimen is reduced to the fourth premolar and the third true molar and eventually to the last true molars alone. Thus, both in the great complexity of the back molars and the fact that the anterior teeth are worn out and then discarded, the wart-hog affords a parallel to the anomalous dentition of the elephant.

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* The characters and eruption of the teeth of the pig are so constant that it is possible to identify the age of the animal with comparative certainty.—H. W. M. T.

The last molar is implanted in the jaw to a great depth, and shows little tendency to form roots; hence it approaches to being a tooth of persistent growth.

Phacochœrus presents the peculiarity that the tusks are large in both sexes.

The upper canines in the boar turn outwards and finally upwards, so as to pass outside the upper lip; this peculiarity in direction, yet more marked in *Phacochœrus*, attains its maximum in the *Sus babirussa.*

Sus babirussa.—This creature, strictly confined to the Malay Archipelago, where it frequents woody places, has (in the male) the upper and lower canines developed to an enormous extent. The upper canines are turned upwards so abruptly that they pierce the upper lip, instead of passing outside it, as in other *Suidæ,* preserve a nearly upright direction for some little distance and then curve backwards, so that their points are directed almost towards the eyes.

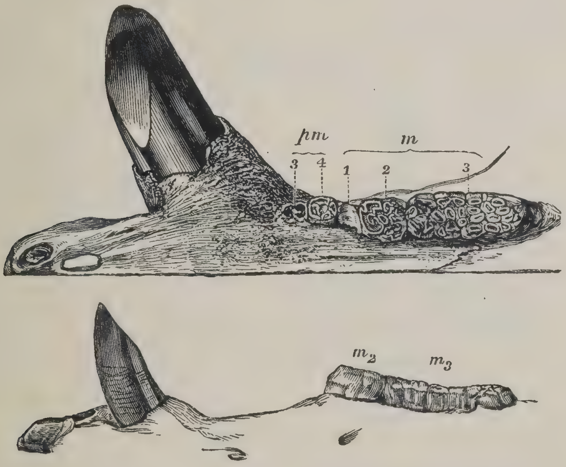

Fig. 281.—Upper and lower teeth of *Phacochœrus*. In the upper jaw the last two premolars and the much-worn first true molar remain. In the lower all have been shed off, save the last two true molars. From a specimen in the Museum of the Royal College of Surgeons.

The lower canines are less aberrant in direction and in shape, being somewhat triangular in section, but they also are of very great length and pass upwards, far above the level of the snout; their points are directed backwards, but have in addition an outward inclination. The canines are devoid of enamel, and grow from persistent pulps, a fact which sometimes has a disastrous result, for the tip of the tooth, occasionally taking a wrong direction, re-enters the head or the jaws of the animal.

Their length is very great; though the animal is smaller than the domesticated pig, its canines attain a length of eight or ten inches. Their use is a matter of conjecture; the position of the upper tusks has suggested the idea that they may serve as a protection to the creature's eyes as it seeks its food, consisting of fallen fruits, among the brushwood. But were that the case the female also would probably have them, which is not so, the upper canine being only about ·75 inch long, though it is everted and is beginning to turn upwards; the lower tooth is a little larger; and although in old animals they are often broken off, it is not certain that they are much employed in fighting. Its other teeth are in no respects remarkable.

The natives of Fiji make use of the persistent growth of the tusks of the pig to procure as ornaments tusks which have grown into a ring; this is effected by extracting or breaking off the opposing upper tooth.

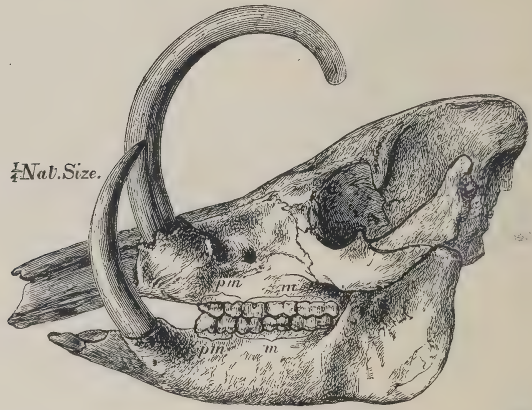

Fig. 282.—Skull of *Sus babirussa* (male). The upper incisors have been lost from the specimen figured; they are much like those of a pig.

Hippopotamus.—The dental characters, as well as others, indicate the affinity of the *Hippopotamus* to the *Suidæ*:—

$$i\,\frac{2}{2}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{3}{3}.$$

The incisors are tusk-like, and bear but little resemblance to those of most other mammalia; they are nearly cylindrical, bluntly pointed at their apices by the direction of wear, and this is in some measure determined by the partial distribution of the enamel, which is laid on in longitudinal bands in the upper teeth, but merely forms a terminal cap on the lower incisors.

The upper teeth, standing widely apart, are implanted nearly vertically; the lower incisors, of which the median pair are exceedingly large, are implanted horizontally.

The canines are enormous teeth; the lower, as in the hog, are trihedral, and are kept pointed in the same manner; the upper canines are not so long, and the portion exposed above the gum is relatively short.

The incisors and canines are all alike teeth of persistent growth.

The premolars, of which the first is lost early (being, like the similar tooth in the pig, perhaps a milk molar), are smaller and simpler teeth built up on the same type as the true molars.

These latter, especially when worn, have a very characteristic double trefoil pattern; the four cusps, in the first instance, were separated by a deep longitudinal and a still deeper transverse groove; each cusp was, moreover, trilobed. The first result of wear is to bring out the appearance of four trefoils. Next, when the longitudinal furrow is worn away, two four-lobed figures result; and finally all pattern becomes obliterated, and a plain field of dentine surrounded by enamel alone remains.

The teeth of the *Hippopotamus* are subject to a great amount of attrition, as is well shown by a specimen presented to the Museum of the Odontological Society, in which the molar teeth are all excessively worn. The Hippopotami use their incisors and canine tusks for the purpose of uprooting aquatic plants, of which their food mainly consists; the roots of these are, of course, mixed up with much sand, which wears down the teeth with great rapidity. The larger incisors and the canines are, and for centuries have been, articles of commerce, the ivory being of very dense substance and useful for the manufacture of small objects.

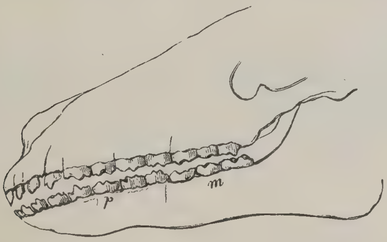

Fig. 283.—Side view of the dentition of *Anoplotherium*. (After Owen.)

Anoplotherium, from the Upper Eocene of Europe, is a genus of interest to the odontologist, because it possessed the full typical mammalian dentition as far as the number of teeth went; they were of nearly uniform height, none strongly differentiated from those nearest to them, and they were set in close contiguity with one another, so that there was no "diastema."

The lower molar teeth of the *Anoplotherium* are built up on the same type as those of the *Rhinoceros*, and present the same double crescent; the upper molars are also referable to the same fundamental forms, though the difference is greater. The laminæ (transverse ridges), oblique in the *Rhinoceros*, are in *Anoplotherium* still more oblique, so that they become more nearly parallel with the outer wall, and an accessory pillar is developed at the inside of the anterior laminæ.

Not very widely removed from *Anoplotherium* is *Oreodon* (*Cotylops*), an ungulate also of Eocene age.

Like a good many tertiary ungulates (both artiodactyle and perissodactyle), it had the full typical number of teeth, forty-four; but its interest to the odontologist is enhanced by the co-existence of strongly marked canines with molars very much like those of ruminants, a group almost always devoid of canines.

Oreodon had

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;pm\,\frac{4}{4}\;m\,\frac{3}{3},$$

i.e., the typical number of each kind of teeth. But in the lower jaw the first *four* teeth are like incisors, and the tooth which is like a canine is not the tooth corresponding to the upper canine, but to the small upper first premolar.

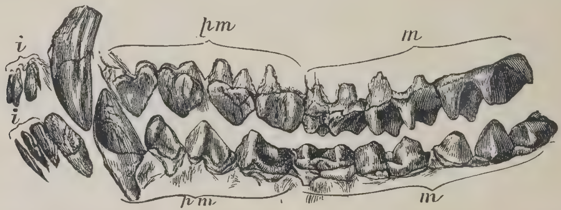

FIG. 284.—Upper and lower teeth of *Oreodon culbertsonii*. (After Leidy, "Smithsonian Contributions," 1852.)

This is a fair illustration of the fact that, although in nature it is generally the same tooth which is modified to perform the function of a canine, it is not invariably the case; for here in the same animal are two different teeth in the upper and lower jaws thus respectively modified. And as they are different teeth, it happens that the upper canine closes in front of the lower.

The same thing has been observed by Cope in an extinct creature (*Hypertragulus*) allied to the chevrotains.

There is reason to believe that there was some difference in the size of canines between the male and female *Oreodon*.

The remaining artiodactyle ungulates (selenodont) are divided into the Tylopoda (camels), the Pecora and Traguloidea, though the transitional forms linking the bunodont Ungulata with the selenodonts are abundant in the Tertiary epoch.

The **Camels** have both upper incisors and canines, the dental formula being:—

$$i\,\frac{1}{3}\;c\,\frac{1}{1}\;p\,\frac{3}{2}\;m\,\frac{3}{3}.$$

The first two pairs of upper incisors are absent, but the third or outermost pairs are present, and are rather caniniform in shape. In quite young skulls six upper incisors are present, but the two inner pairs are lost very early. The canines are strong pointed teeth, and the lower canine stands well apart from the three incisors of the lower jaw, unlike the fourth tooth in the front of the mandible of typical pecora. (See Fig. 287.)

Of the three premolars which are found in the upper jaw the first (probably pm¹) is close behind the canine; it is not replaced, is not acquired till about the sixth or seventh year, and persists through the life of the animal, and as there is said to be a trace of a follicle of a milk tooth preceding it, it belongs doubtless to the second series.

The second premolar is absent, the third being separated by a long interval from the first. The third premolar is sometimes lost early, but the fourth persists.

The molars of the camel are of the "selenodont" type, a type the derivation of which from the several cusps of a bunodont type is sometimes fairly obvious, but in other cases is more obscure. Thus Scott points out that in the case of some premolars the inner crescent appears to be derived from a folding round of the edges of the outer cusp, which is clearly the protocone; whilst in others it appears to be derived from the occurrence of extra cusps.

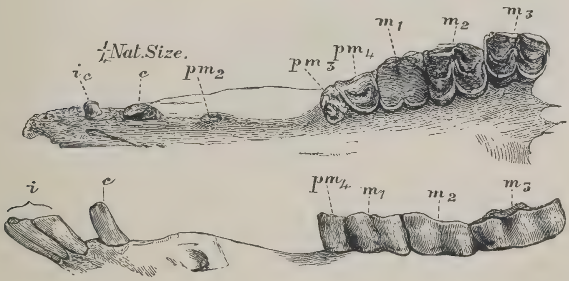

FIG. 285.—Upper and lower teeth of a camel. In the figure pm¹ is lettered as pm², this being the former view of its homology.

The molars of the camel have double crescentic crowns, which may be taken as fair examples of simple ruminant patterns, accessory pillars, &c., being added in some of the other families.

The **Traguloidea,** or Chevrotains, sometimes called Pigmy Musk Deer, in some respects intermediate between the pigs and deer, though zoologically distinct, do not differ in their dentition from the true ruminants, with which they may be noticed here; the upper canines are well developed, especially in the males.

The hollow-horned ruminants (**Sheep** and **Oxen** and **Antelopes**), and likewise almost all the solid-horned ruminants (**Deer**), have the following dental formula:—

$$i\,\frac{0}{3}\;c\,\frac{0}{1}\text{ or }c\,\frac{1}{1}\;p\,\frac{3}{3}\;m\,\frac{3}{3}.$$

The lower incisors are antagonised not by teeth, but by a dense gum which clothes the fore part of the upper jaw. If a sheep be watched as it feeds, it will be seen to grasp the blades of grass between the lower teeth and the gum, and then to tear them off by an abrupt movement of the head, as it would be impossible, strictly speaking, for it to bite them off.

The anomaly of the entire absence of upper incisors was held to have been diminished by the statement of Goodsir, who believed that uncalcified tooth-germs were to be found in the fœtuses of many species. As this was precisely what might have been expected, it has since that time passed current as an established fact; but M. Pietkewickz, working in the laboratory of M. Ch. Robin, has absolutely denied the occurrence of even the earliest rudiments of tooth-germs in this situation, after an examination of a series of fœtuses of the sheep and cow ranging even from the earliest periods (⁷).

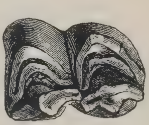

Fig. 286.—Selenodont molar of a deer.

Miss F. Mayo (⁶) has re-examined this subject. She confirms the view that the germs are absent, but she points out that in the region of the missing canine differentiation proceeds a little further than in the incisor region, though it never attains to the formation of a real tooth-germ, *i.e.*, that the suppression of the teeth has been progressive, and that the canine has been lost at a later period than the incisors. She bases this idea upon the occurrence of those knobs of epithelium which one is accustomed to find where an enamel-germ is atrophying. Very numerous figures are given, so that the reader may judge for himself of the material from which the conclusions are drawn.

Grouped with the six incisors of the lower jaw, and in no respect differing from them, rise the pair of teeth which are very arbitrarily termed "canines." No attempt can be made to do more in these pages than give a bare outline of generally well-known facts. The usual dental formula has been retained,

$$i\,\frac{0}{3}\;c\,\frac{0}{1}.$$

Although the absence of upper canine teeth is a very general characteristic of ruminants, rudimentary canines exist in some deer, and the author is indebted to the kindness of the late Sir Victor Brooke, a high authority upon the *Cervidæ*, for the following note :—

"The upper canines are present in both sexes in all the species of *Cervidæ*, with the exception of *Alces*, *Rangifer*, *Dama*, some smaller species of *Rusa*, *Axis*, *Capreolus*, *Cariacus*, *Blastocerus*, *Coassus*, and *Pudu*. The upper canines, when present, are, with the notable exception of *Moschus*, *Elaphodus*, *Cervulus*, and *Hydropotes*, small laterally compressed rudimentary teeth. Their crowns are in about the same stage of reduction as the crowns of horses' canines, but their roots are relatively much more reduced." Hence they are often lost in dried skulls, and it has generally been supposed that but few deer possessed canines at all.

The hornless musk deer (*Moschus*) possesses upper canines of most formidable dimensions, while the female has very small subcylindrical canines.

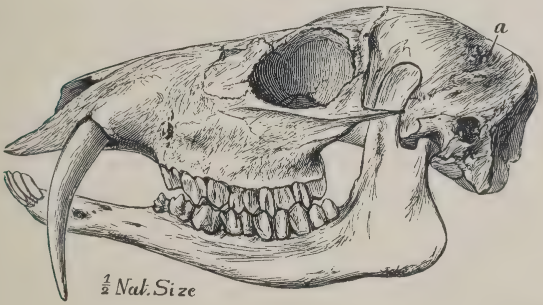

FIG. 287.—Cranium of male musk deer (*Moschus moschiferus*).

The male pigmy musk deer (*Tragulus*) has large canines of persistent growth, the female small canines with closed roots.

The Indian Muntjac deer (*Cervulus*) has somewhat small horns, which are perched upon persistent bony pedicles, and it has upper canines which are curved outwards from beneath the upper lip, much as are the tusks of a boar ; they do not, however, grow from persistent pulps, and are absent in the female.

Cuvier first pointed out that there was a relation between the presence of horns and the absence of canine teeth ; the latter, serving as weapons of sexual combat solely and being probably in no other way of service to the animal, are not required by an animal provided with powerful antlers or horns, whereas the absolutely hornless musk deer would be totally unprovided with weapons of offence were it not for his canines. To the musk deer and the Muntjac must be added Swinhoe's water deer, *Hydropotes inermis*, which has canines shorter and stouter than *Moschus*, and Michie's deer, *Elaphodus cephalopus*, another small hornless species, of which the males are furnished with formidable canine teeth which are not so long as the *Moschus*, but are flattened from side to side, and are very strong.

Although, with the foregoing exceptions, all the deer, oxen, sheep, antelopes, and the giraffe, animals constituting the greater number of the Ruminantia, are without canine teeth, yet in the *Camelidæ* tusk-like canines are met with.

It is a character of the artiodactyle Ungulata that the premolar teeth are of decidedly simpler form than the molars. In the ruminants the premolars may be said each to roughly correspond to one half of a true molar, and the premolars and molars form a continuous series.

In all true ruminants the last true molar of the lower jaw has a third lobe,* and the line of the outer surface of the row of teeth is rendered irregular by the anterior edge of each tooth projecting outwards slightly more than the posterior border of the one in front of it. The deviations in the patterns of the surfaces of the molar teeth are so constant and characteristic that, although the common ruminant pattern is preserved in all, it is often possible to refer an individual tooth to its right genus.

The ruminants all have a well-developed milk dentition, which serves the animal for a long time, indeed until after it has attained to its adult dimensions ; thus a sheep has not completed the changing of its teeth till the fifth year, and a calf till the fourth year. But the first permanent molar is in them, as in so many other animals, the first of the permanent set to be cut, and comes up in its place at the sixth month (in the lamb), and hence has a long period of wear before any of the other second teeth are cut. Consequently the first permanent molar is, as seen in Fig. 285, invariably worn down to a much greater extent than the other permanent teeth ; in the specimen figured it has been worn down below the inflections of enamel, so that it has lost its roughened grinding surface, and is reduced to a smooth area of dentine.

Not much is known of the structure of the dental tissues of the Ungulata which calls for mention in an elementary work. The thick cementum of the crown of the teeth of the horse, and indeed of most of the group which possesses thick cement, contains many "encapsuled lacunæ," and is perhaps developed from a distinct cement-organ of cartilaginous consistence.

In the *Cervidæ* the true molars are somewhat brachyodont, and these teeth take their place at once with the neck at the level of the margin of the gums, and remain at this level ; the folds of the teeth are not much filled up with cementum.

In the *Bovidæ* teeth tend to be more hypsodont, and the tooth goes on growing up while a considerable part is worn away, so that the crown is lengthened and the root small ; in this type of tooth the interstices of the columns are filled up with cementum.

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* Sir Victor Brooke informs the author that *Neotragus hemprichii*, a small Abyssinian antelope, has only two lobes to the third lower molar.

The hypsodont tooth being in some respects a further elaboration of the brachyodont, we find, as might be expected, that in the early and more generalised forms the teeth are shorter than in those which occur later, and every transition between the two may be found both in the artiodactyle and perissodactyle Ungulata (Flower and Lydekker).

Perissodactyle Ungulates.—These are much less numerous than the artiodactyles, and amongst recent animals comprise only the tapir, the horse, the rhinoceros and their allies.

In the Tertiary period, however, there were a much larger number, some of which bridge over existing gaps, and others of which became specialised along lines which have died out.

Their premolars and molars form an unbroken series; they are big, ridged or further complicated by various foldings, and the premolars, at all events the last three of them, are as complex in pattern as the true molars. The crown of the last molar is generally bilobed, and the tooth immediately behind the canine comes but once in the horse. In the rhinoceros it is sometimes replaced, but sometimes the milk tooth persists, while in the horse this tooth is never replaced; nevertheless it appears to belong to the second series, as it is not cut until about the thirtieth month, that is to say, after the milk molars, and but shortly before the eruption of the second and third premolars (see p. 467).

The molar teeth are kept in an efficient state of roughness by the enamel dipping deeply into the crowns, by the cusps, in fact, being of very great depth. It consequently happens that after the immediate apex is worn away the flattened working face of the tooth is mapped out into definite patterns. These have been studied with great care on account of the light thus thrown upon fossil remains, often consisting of little else than the teeth. The result has been to establish a general community of type, so that, dissimilar as they at first sight appear, it is possible to derive all, or almost all, the configurations of their crowns from one or two comparatively simple patterns. But odontologists are not yet agreed, or rather are only getting to know enough of the vast number of ungulates which once existed (of which many have only lately been discovered) to decide with certainty what the parent pattern was.

The patterns of the molars have been made use of to divide them into the following groups:

(i.) Bilophodont, *i.e.*, two ridges, *e.g.* the tapir.

(ii.) Molar (lower) bicrescentic, *e.g.* rhinoceros.

(iii.) Lower molar bicrescentic, with the addition of inner lobes or columns, *e.g.* horse.

The tapir is interesting as appearing in Miocene strata and remaining practically unchanged till the present time, being thus the oldest existing genus of mammals (Flower).

Tapir.—The dental formula is

$$\text{i}\,\frac{3}{3}\;\text{c}\,\frac{1}{1}\;\text{p}\,\frac{4}{3}\;\text{m}\,\frac{3}{3}.$$

In a brief survey, like that to which the present work is necessarily confined, it will suffice to mention that there is no great peculiarity about the incisors or the canines, save that the third upper incisor is larger than the canine, and opposes the lower canine which ranges with the lower incisors; behind the canine comes an interval, after which come the premolars and molars, which are interesting as being of simpler pattern than those of most ungulates; and it will be necessary to very briefly allude to the various patterns characteristic of ungulate teeth, with a view of showing how they may have been derived the one from the other.

The first upper premolar is triangular, one of its cusps being suppressed, but the rest of them are more or less square and resemble true molars. It has been preceded by a milk tooth, so that it is certainly of the second series. Four cusps are traceable in the molar teeth, but ridges uniting the two anterior and the two posterior cusps are strongly developed, at the cost of the antero-posterior depression, *i.e.*, of one of the arms of the cross which separate the four cusps in other quadricuspid molars. There is therefore only a deep transverse fissure (hence it is called a bilophodont tooth), and the quadricuspid form is disguised. A low wall on the outside of the tooth connects the two ridges.

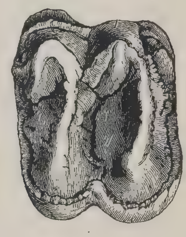

Fig. 288.—Molar tooth of tapir.

Thus the protocone and paracone are joined to form the anterior ridge or protoloph, and the metacone and hypocone to form the posterior or metaloph, whilst a "style" is added in front of the paracone.

According to the advocates of the tritubercular theory, the cusps present would be the protocone, paracone, metacone and hypocone, united in pairs by transverse ridges.

In **Rhinoceros,** the number of incisors varies, they being often almost rudimentary and not persistent, so that it is difficult to assign a dental formula to them :—

$$i\,\frac{?}{?}\;c\,\frac{0}{1\ ?}\;pm\,\frac{4}{4}\;m\,\frac{3}{3}.$$

In some fossil forms there are three lower incisors and a canine, so that it seems probable from comparison with them that the front lower tooth of the recent animal is the canine.

The first upper premolar is in some cases a replacing tooth; but in others, where the successional tooth is suppressed, the milk tooth persists.

In some of the earlier (Miocene) rhinoceroses the first and second milk premolars are said to persist.

In the molars the external crest or ridge feebly present in the tapir becomes quite complete, the transverse ridges persisting, but becoming oblique; hence the valley between the ridges *c* and *d* is also oblique, and a second valley comes in behind the posterior ridge.

The simplicity of the pattern is also departed from by the margins of the ridges, and therefore the boundaries of the depressions, being waved and irregular.

The lower molars of the rhinoceros are made up of two crescentic ridges, one in front of the other, with the hollows turned inwards. It is less obvious how this pattern is derived from that of the tapir, but it may be that the transverse ridges of the tapir-type of tooth may have become curved and crescentic, so that the original outer edge of the posterior ridge abuts against the back and exterior of the ridge in front of it. The valleys between the processes of enamel and dentine of the tooth of the rhinoceros, termed "sinuses," or *fossettes*, are not filled up solidly with cementum.

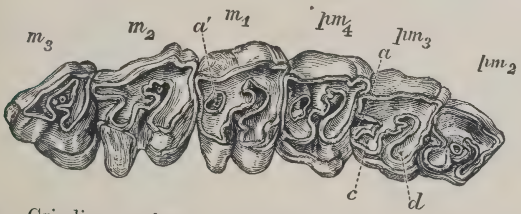

FIG. 289.—Grinding surfaces of upper molar series of a rhinoceros. *a*. Posterior sinus, which at *a′* has become an island by wear. *c*. Posterior ridge or metaloph. *d*. Anterior ridge or paraloph.

Equus.—The horse is furnished with the full mammalian number of teeth, the dental formula being

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{3}{3}.$$

The canines are rudimentary in the female, whilst in the male they are well developed (in the gelding they are of the same size as in the entire horse); and the first premolar, which has no predecessor, is also rudimentary and is lost early. A considerable interval exists between the incisors and the premolars and molars, which latter are very similar to one another, both in shape, size, and in the pattern of the grinding surface.

Mares occasionally have all four canines, but more commonly they have only the lower ones.

The incisors of the horse are large, strong teeth, set in close contact with one another; the teeth of the upper and lower jaws meet with an "edge to edge bit," an arrangement which, while it is eminently adapted for grazing, leads to great wearing down of the crowns. An incisor of a horse or other animal of the genus may be at once recognised by that peculiarity which is known as the "mark."

From the grinding surface of the crown there dips in a deep fold of enamel, forming a *cul de sac*. As this pit does not extend the whole depth of the crown, and the incisors of a horse are submitted to severe wear, the fold eventually gets worn away entirely, and the worn surface of the dentine termed the "table" presents no great peculiarity. But as this wearing down of the crown takes place at something like a regular rate, horse dealers are enabled to judge of a horse's age by the appearance of the mark upon the lower incisors. The "mark" exists in *Hipparion*, but not in the earlier progenitors of the horse. It is found in no other animal except a South American mammal of doubtful affinities—*Macrauchenia*.

A horse attains to its adult dentition very slowly. A foal is born with the two first incisors in each jaw; when nine weeks old it has four.

At 2½ years the temporary first incisors are shed, at 3½ the second, and at 4½ the third incisors; and at 5 years the horse is said to have a "full mouth," the corner teeth having sharp edges. As the rate of wear is equal, the mark gets worn out soonest upon the central incisors, and last upon the corner teeth.

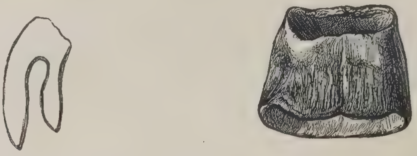

FIG. 290.—Apex of crown of an upper incisor of a horse, not yet completely formed.

At six the age is judged of chiefly by the wear of the corner teeth, as the cavity in the centrals is nearly worn out. At the eighth year the central table is rather triangular, and the cups are gone from the second incisors entirely, while from 8 to 10 years a stain remains on the first incisors, and a round ring of enamel on the corner teeth.

After 12 years the mark has wholly gone, and there is no certainty as to age as far as it is concerned.

After the "mark" is worn away the centre of the tooth is marked by a difference of colour, due to the presence of secondary dentine, into which the remains of the pulp have been converted; this lies in front of the site of the mark.

It is pointed out by Sydney Galvaine ("Horse Dentition") that there is another reliable sign of age which comes into play after the wearing out of the cups of the lower teeth.

Upon the front surface of the upper incisors is a longitudinal median groove, which extends the whole length of the implanted portion, but stops short of the point of the crown.

Upon the first and second incisors it is variable, but on the upper corner teeth it just appears at the margin of the gum in a ten-year-old. At this time there is about an inch of crown in view above it, and it takes eleven years to wear away this inch of tooth substance; so that at twenty-one years it reaches the working surface of the tooth. From what has just been said the reader will have inferred that the horse's incisors continue to be extruded from their sockets during the whole of its life, so as to meet the wear which is taking place.

But they are not teeth of persistent growth in the ordinary sense, as the roots taper down to blunt points, and their full length is practically complete by the fifth year. It is, therefore, a process of gradual extrusion of an already fully formed tooth. It has been pointed out by Sir John Tomes that the enamel on the front of the tooth extends down to within a short distance from the end of the root; on the back of the tooth it stops short much sooner. It is, however, overlaid by cementum, and is only brought into view upon the exposed crown of the tooth by the wearing away of this softer cementum, so that its existence has not been generally noticed. As the sides of the teeth are not exposed to wear, the cementum covering remains upon them, nearly up to the working surface, while upon the back of the tooth again it is worn off, but only down to a point about three-quarters of an inch above its level on the front of the tooth.

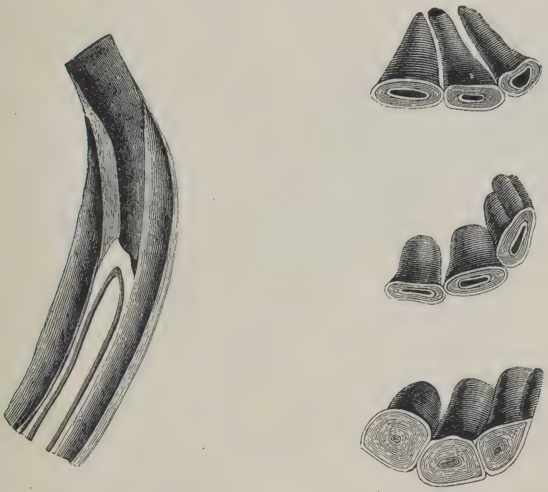

Fig. 291.—Incisors of a horse, showing the marks at various stages of wear.

While in the normal dentition the horse has only three persistent premolars, yet a fourth, sometimes called a "wolf's tooth," is present at the front of the row, a remnant of the fuller dentition of *Palæotherium* and *Hipparion.*

When a bit is put into a horse's mouth it rests in the interval, or diastema, which exists between the incisors and the commencement of the molar series.

The molars of the horse are remarkable for their great length; they do not grow from persistent pulps, but nevertheless they do go on growing until a great length of crown of uniform diameter is made, subsequently to which the short and irregular roots are formed. As the upper working surface of the crown becomes worn, the tooth rises bodily in its socket, and when by an accident its antagonist has been lost, it rises far above the level of its neighbours. This elevation of the tooth takes place quite independently of growth from a persistent pulp, and, in fact, happens after the formation of its roots.*

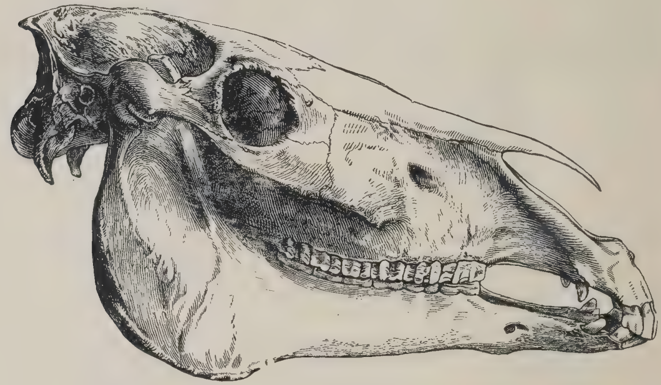

FIG. 292.—Side view of the dentition of a stallion. At a short interval behind the incisors are seen the canines, then, after a considerable interval, the premolar and molar series.

The pattern of the horse's molar has been already described. It should be added that the last molar differs from the rest in its posterior moiety being less developed than in the other teeth. As each ridge and each pillar of the tooth consists of dentine bordered by enamel, and as the arrangement of the ridges and pillars is complex, as, moreover, cementum fills up the interspaces, it will be obvious that an efficient rough grinding surface will be preserved by the unequal wear of the several tissues.

The milk teeth, as in all the Ungulata, are very complete, and are retained late; they resemble the permanent teeth in general character, but the canines of the horse are rudimentary in the milk dentition, as might have been expected, their greater development in the male being a sexual character.

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* The same phenomenon has been observed, under similar conditions, in human teeth.—H. W. M. T.

If one had specimens of most of the ungulates which ever lived, there would be no doubt as to the relationship of the various patterns of the molar teeth; as it is, one is embarrassed by the lack of the material, which leaves gaps in some places too great to bridge over without some amount of speculation. Sir W. Flower divides the principal varieties (¹) into three :—

(i.) That in which the outer wall is feebly developed, and transverse ridges become the prominent features, as in the tapir.

(ii.) That in which the outer wall is greatly developed and more or less smooth, the transverse ridges being oblique, as in the rhinoceros.

(iii.) That in which the outer surface and edge of the outer wall is zigzagged, or bicrescentic, as in the horse and *Palæotherium.*

To the perissodactyle ungulates, which are specially interesting on account of their dentition, must be added *Homalodontotherium*, a Tertiary mammal of as yet uncertain affinities, the remains of which were described by Sir W. Flower (*loc. cit.*).

It had highly generalised characters: its teeth were arranged without any diastema, and the transition in form from the front to the back of the mouth was exceedingly gradual, so that no tooth differed much from those on either side of it. Taking the pattern of its molar teeth alone into account, it would have been without hesitation declared to be very nearly allied to *Rhinoceros*, on which type they are formed, but the resemblance fails in the canine and incisor region, and it must be considered to be one of those generalised types related to *Rhinoceros*, to *Hyracodon*, and perhaps connecting them with such aberrant forms as *Toxodon.*

The largest of ungulates more or less akin to the perissodactyles equalled the elephant in size, and have been named by Professor Marsh *Brontotheridæ* or *Titanotheridæ*. The dental formula was

$$i\frac{2}{2}\ c\frac{1}{1}\ pm\frac{4}{3}\ m\frac{3}{3}.$$

The incisors were small and sometimes deciduous, and the canines short and stout, the lower being the more conspicuous owing to their being separated by a slight diastema from the premolars, which is not the case in the upper jaw.

The premolars in both jaws increased in size from before backwards, and did not differ from the molars next them. In the lower jaw the premolars and molars all consisted of two crescents, save the last, which had three crescentic cusps, and so were of the *Palæotherium* type. The molar teeth stood apart from those of any recent perissodactyles in their huge size, the square last upper molar, for example, measuring four inches antero-posteriorly and more than three transversely (Marsh (⁴)).

Amblypoda (Dinocerata).

In the same region which yielded the toothed birds (Eocene formations of Wyoming), the fossil remains of many huge animals have been discovered, for which new orders have been proposed by Professor Marsh (*loc. cit.*), it being impossible to classify them under any existing order. The Dinocerata were creatures nearly as large as elephants, and presenting some sort of resemblance to them in general form; they were remarkable for the relative smallness of their brains, which could apparently have been drawn through the canal of the vertebral column. They present points of resemblance to the perissodactyle Ungulata, and also to the Proboscidea, to which they were at first referred, though their affinities are rather with the former.

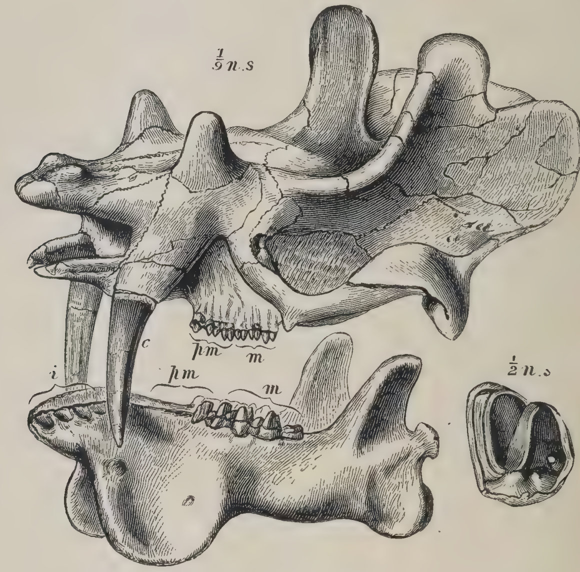

Fig. 293.—Upper and lower jaws of *Dinoceras* (Marsh).

The dental formula was

$$i\,\frac{0}{3}\;c\,\frac{1}{1}\;pm\,\frac{3}{3}\;m\,\frac{3}{3}.$$

In Professor Marsh's words, "the superior canines are long, decurved, trenchant tusks. They are covered with enamel, and their fangs extend upwards into the base of the maxillary horn-core. There is some evidence that these tusks were smaller in the females. Behind the canines there is a moderate diastema. The molar teeth are very small. The crowns of the superior molars are formed of two transverse crests, separated externally, and meeting at their inner extremities. The first true molar is smaller in this specimen than the two preceding premolars. The last upper molar is much the largest of the series.

"The lower jaw in *Dinoceras* is as remarkable as the skull. Its most peculiar features are the posterior direction of the condyles, hitherto unknown in Ungulata, and a massive decurved process on each ramus extending downward and outward below the diastema.

"The position of the condyles was necessitated by the long upper tusks, as, with the ordinary ungulate articulation, the mouth could not have been fully opened. This low position of the condyle, but little above the line of the teeth, is a noteworthy character. The long pendent processes were apparently to protect the tusks, which otherwise would be very liable to be broken. Indications of similar processes are seen in *Smilodon* and other carnivores with long upper canines. With the exception of these processes, the lower jaw of *Dinoceras* is small and slender. The symphysis is completely ossified. The six incisors were contiguous, and all directed well forward. Just behind these, and not separated from them, were the small canines which had a similar direction. The crowns of the large molars have transverse crests, and the last of the series is the largest."

It would appear possible that the eminences shown in the figure, and spoken of as "maxillary horn-cores," may be merely the extended sockets of the teeth, which would otherwise have had an implantation inadequate to their length; they are, however, described as solid, except at their bases, where they are perforated for the root of the canine tusk, which would look as though they were truly horn-cores; moreover, the *Brontotheridæ* had horn-cores equally peculiar in position (*i.e.*, on the maxillary bones).

Tinoceras, another genus, had a very long and slender canine, also protected when the mouth was closed by a downward prolongation of the lower jaw as in *Dinoceras*.

Another extraordinary creature discovered by Marsh is *Protoceras*. It appears, according to Osborn and Wortman, to have affinities with the Pecora and Tragulina, and belongs to the artiodactyle section of the ungulate order.

It had no upper incisors, but was possessed of large trihedral canines in the upper jaw; the lower incisors and canines ranged together as in ruminants, and were of spatula-like shape; the molar teeth were selenodont and brachyodont.

The female was possessed of canines, but they were only half the size of those of the male, and the skull of the female was smooth, though that of the male fairly bristled with ten bony prominences, upon which, however, there appear not to have been any true horns.

Although *Protoceras* was really quite distinct from the Dinocerata, being an artiodactyle, the general aspect of the skull, with its prominences and its dentition seen in side view, much resembled *Dinoceras*, thus affording a striking case of "parallelism."

Many of the lower Eocene types, *e.g.*, *Periptychus*, *Conacodon*, *Pantolambda*, &c., have triangular trituberculated molars. They are very primitive animals, and are regarded by Matthew as belonging to a group ancestral to the typical Condylarthra and Amblypoda, but much more primitive than the latter and not easily separated from the former.

Condylarthra.

These animals, though contemporaneous with the Amblypoda, possessed teeth of a quadritubercular instead of a tritubercular pattern.

They were smaller and more generalised ungulates, with affinities both with the articdactyle and the perissodactyle groups. They usually had the full mammalian dental formula, and the molars were brachyodont, and generally bunodont. The premolars were simpler than the molars, and tritubercular teeth were common in the group.

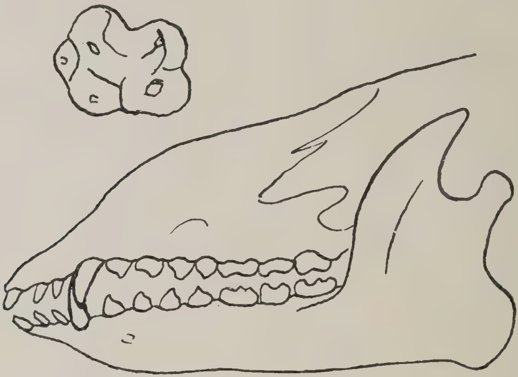

FIG. 294.—*Phenacodus primævus* (half natural size). (After Cope.) The grinding surface of a lower molar is represented above.

Cope has suggested that the ancestors of the lemurs are to be found in this group, whilst the genus *Phenacodus* is perhaps the source whence the line of modification ending in the horse has been derived. It also comes near to the *Hyracoidea*, so that it is a highly generalised form, and Cope regards it as the ancestor of all ungulates, though not of all placental mammals, inasmuch as its molars were already quadritubercular. But he points out that one has to go back but a short time to find its tritubercular ancestors, so that it is but a little way from what may be regarded as the common stock.

Phenacodus had a dental formula—

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;pm\,\frac{4}{4}\;m\,\frac{3}{3}.$$

The incisors were somewhat expanded transversely, and the canines were not very large, the inferior incisors being directed somewhat obliquely forwards, and the front part of the jaw was weak. The premolars stood a little apart, the first having only one root and a simple crown, the others bearing an internal lobe and two external cusps. The upper molars had four cusps, two external and two internal, with, in addition, two slight intermediate cusps and a narrow cingulum. The lower molars had four cusps like those of the upper and a small odd one behind.

The small isolated cusps which occur between the principal ones develop in later forms into cross ridges connecting the outer and inner cusps, and so produce a lophodont molar.

Toxodontia.

The existing ungulate animals form only a small proportion of those once peopling the earth, and many extinct forms have been discovered, which, while forming affinities with the Ungulata, can yet hardly be classified under any existing order. For example, *Toxodon*, a creature equalling the hippopotamus in size, which was discovered by Darwin in late Tertiary deposits of South America, has a dentition recalling in some respects the *Bruta*, in others the rodents.

Its dental formula was—

$$\mathrm{i}\,\frac{2}{2}\;\mathrm{c}\,\frac{?\,0}{1}\;\mathrm{p}\,\frac{4}{3}\;\mathrm{m}\,\frac{3}{3},$$

the median pair of upper incisors being small, the outer exceedingly large, with persistent pulps and long curved sockets, extending back to the region of the molars, just as in existing rodents.

In the lower jaw there were three pairs of incisors, subequal in size, and growing from persistent pulps ; they resemble the incisors of rodents in having a partial investment of enamel, but differ from them in being prismatic in section, and in having the enamel disposed on two sides of the prism.

The molars were also very remarkable ; they grew from persistent pulps and had curved sockets, but the curvature of these was in the reverse direction to that which obtains in rodents, *i.e.*, the convexity was outwards, and the apices of their roots almost met in the middle line of the palate ; it was this peculiarity that suggested the name.

Another peculiarity in the molar teeth, in which they stand quite alone, is that, like the incisors, they have a partial investment with enamel, those referred to the premolar series having it confined to their outer surfaces, while the three back teeth of the molar series had a plate also laid on to their inner surfaces.

In the interval between the incisors and molar series canines have been found in the lower jaw ; they were sharp-edged, and had a partial distribution of enamel over their surface. In an upper jaw alveoli for canines were found, but the teeth themselves are not known.

Another animal from the same locality (*Mesotherium* or *Typotherium*) had somewhat similar characters, though it was not nearly so large; it had the dental formula

$$i\frac{1}{2}\ c\frac{0}{0}\ pm\frac{2}{1}\ m\frac{3}{3},$$

the incisors (of persistent growth) standing apart from the premolar and molar series just as in the rodents. It is remarkable that this animal, which possessed a clavicle, in its skeleton also shows on the one hand generalised ungulate characters, and on the other resemblances to the rodents.

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CHAPTER XIX.

HYRACOIDEA, PROBOSCIDEA AND SIRENIA.

The Teeth of Hyracoidea.

The Biblical coney (*Hyrax*), an animal as large as a rabbit, must not be passed over without mention, as its dentition has been indirectly the source of much controversy. So far as the pattern of its molar teeth goes, it corresponds closely with the rhinoceros, and was hence classed in close proximity to that genus by Cuvier. But a more extended survey of its characters has led to its being placed in a separate order. It is a good example of the danger which attends relying upon any single character, such as the pattern of the teeth, as being alone a sufficient basis for classification.

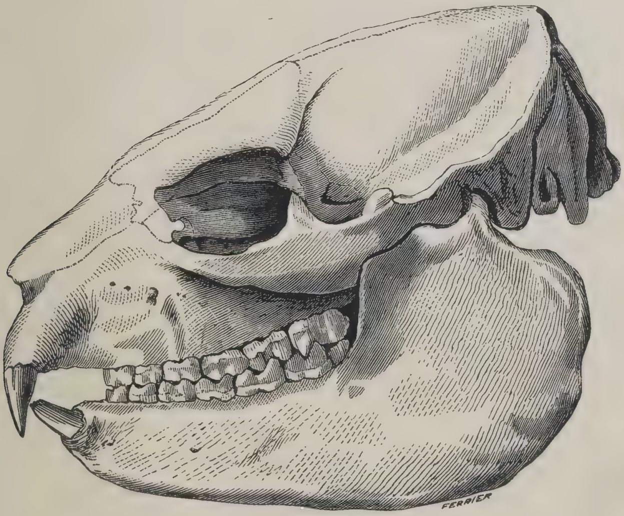

Fig. 295.—Skull of the *Hyrax*.

All observers, however, are not agreed as to its position; it certainly presents affinities with perissodactyles, but modern zoologists are pretty well agreed in placing it in an order by itself. Cope, however, regards it as closely akin to some early highly generalised ungulates, which he groups together by the name of *Taxeopoda*; they all possessed five toes on each foot, and many of the characters of their teeth bring them within measurable distance of ancient Insectivora.

The dental formula is $i\frac{2}{2}\ c\frac{0}{0}\ pm\frac{4}{4}\ m\frac{3}{3}$.

Seen from the side, the dentition bears some resemblance to that of a rodent, because of the size of its great incisors, which grow from persistent pulps, are chisel-edged, prismatic in section, and are furnished with a very thick coat of enamel on their antero-external and postero-internal faces. The second pair of incisors, which are small, are soon lost.

In the lower jaw the middle incisors are small, and the outer ones largely developed, and all persist. Their crowns are in a manner trilobed, and they pass in ordinary closure of the mouth behind the upper incisors, where they are met by a dense pad of gum, but they are not of persistent growth.

Hyrax has the full typical number of premolars and molars, and the patterns of these teeth, as already stated, are closely similar to those of the rhinoceros.

The Teeth of Proboscidea.

At the present day the elephant stands alone, removed by many striking peculiarities from the Ungulata, to which it is more nearly allied than to other orders. In former days the order Proboscidea was represented by several genera, widely distributed over the globe, and transitional forms linking the elephant with somewhat less aberrant mammalia were not wanting, for Andrews has discovered in the Eocene and Miocene of Egypt several forms which throw new light upon the evolution of the Proboscidea from more generalised ungulates. In this order the incisors grow from persistent pulps, and form conspicuous tusks; the elephant has $i\frac{1}{0}$; the *Mastodon* had $i\frac{1}{1}$, the *Dinotherium* $i\frac{0}{1}$; and the Egyptian series show the tusks to have been I_2 of the typical mammalian dentition.

Two striking features characterise the dentition of the elephant: the enormous length of the incisor tusks and the peculiar displacement from behind forwards of the molar teeth, by which it results that not more than one whole molar, or portions of two, are in place at any one time.

The upper tusks are preceded by small deciduous teeth; this is well established, though it has been denied by Sanderson. The milk incisors have their bases irregularly closed. They are erupted between the fifth and the seventh months, and are shed before the second year. When first cut they are tipped with enamel, but the enamel cap is soon worn off, and the remainder of the tusk consists of that modification of dentine known as "ivory," and of a thin external layer of cementum. In some extinct species the enamel formed longitudinal bands upon the tusks.

The permanent tooth at the time of its eruption is coated with cementum, even over its enamel tip; this latter is about 5 mm. thick and extends for from 1 to 6 inches along the tusk.

In the Indian elephant the tusks are not so large as in the African species; and the tusks of the female are so much shorter than those of the male as to be insignificant. In the African elephant it has been said that no such difference in size has been established; but, according to Baker, about the White Nile region there is a considerable sexual difference. The Indian elephant subsists largely upon grasses, &c., whilst in Africa grass is often not obtainable, and the elephants overturn trees, chiefly the mimosa, to feed on the foliage, several animals sometimes combining for the purpose. Thus in the case of the African form the tusks have more relation to the procuring of food than in the Indian form, and this may help to account for the relatively large size of the female tusks.

The surfaces of the tusks of the Indian female are often deeply excavated about the level of the edge of the gum, and are sometimes so weakened from this cause that they break off. The late Professor Moseley told the author that he was informed by the late Major Rossall, who as a sportsman had great knowledge of Indian elephants, that the tusks of all the females he had ever seen were so affected, and that the larvæ or pupæ of a dipterous insect were often found imbedded in the gum, and attached to the surface of the tusk. There is a specimen of a female elephant's tusk with the pupæ attached in the Museum of the Royal College of Surgeons. It would be a matter of interest to ascertain whether the larva really eats away the tusk, or whether the wasting of the tusk be due to absorption set up by the irritated gum. If this condition be due to the action of the insect it is difficult to understand why it should occur in the female only.

In Abyssinia the tusks are smaller than in equatorial Africa. Indeed, in parts of Abyssinia the elephants have quite small and short tusks, and amongst Indian elephants males are sometimes met with which have tusks no larger than the females of corresponding size; they go by the name of "Mucknas." This peculiarity is not always transmitted, and it is known that in Ceylon tuskless sires sometimes beget "tuskers." Amongst the Ceylon elephants the possession of large tusks by the male is an exceptional thing, Sanderson stating that only one in three hundred has them, while amongst fifty-one Indian elephants only five were tuskless. The tusks are formidable weapons, and great dread of a "tusker" is shown by elephants less well armed.

The longest, if not the heaviest, tusks were possessed by the mammoth, the remains of which are so abundant in Siberia; these tusks, which were strongly curved, and formed a considerable segment of a circle with an outward inclination, so as to clear well the sides of the head, attained a length of 13 feet, and a weight of 200 lbs. each.

The record tusks, weighing respectively 235 and 225 lbs., came from the Kilmanjaro district in Africa: the larger of these measured 10 feet 4 inches along its convex side, and sold at Zanzibar for £700; prior to this the largest known had measured 9 feet 4 inches. A pair of African tusks shown at the Great Exhibition of 1851 weighed 325 lbs., and measured 8 feet 6 inches in length and 22 inches in circumference, but the average tusks imported from Africa do not exceed from 20 lbs. to 50 lbs. weight. Indian elephants seldom have tusks attaining very large dimensions; one was, however, shot by Sir Victor Brooke with a tusk 8 feet long, weighing 90 lbs.

Ivory is one of the most perfectly elastic substances known, and it is on this account that it is used for billiard balls; it owes its elasticity to the very small size of the dentinal tubes and the frequent bends (secondary curvatures) which they make. To the arrangement of the tubes the peculiar engine-turning pattern of ivory is due. The softer varieties of ivory are said to contain 60·9 per cent. of lime salts, and the harder as much as 64·4 per cent., but these figures, being arrived at by ignition, probably need correction (cf. p. 72) on account of the loss of water of crystallisation. It is interesting to note that in the dentine of the molars, which have more need of hardness and less of elasticity, the percentage of lime salts is nearly as high as in human dentine, viz., 70 per cent. Ivory differs from other dentine in its containing from 34 to 40 per cent. of organic matter (human dentine contains only about 20), and in the abundant concentric rows of interglobular spaces. It is interesting to note in connection with the high percentage of organic matter that the connective tissue basis in ivory is very apparent, especially in secondary formations (Miller). Along these ivory when it decomposes breaks up, so that a disintegrated segment of a tusk consists of detached concentric rings; in this condition many mammoth teeth are found, although sometimes where they have remained frozen and protected from the air until the time of their discovery they are hardly affected by the lapse of the thousands of years which have gone by since their possessors perished.

The best ivory is that which comes from equatorial Africa; Indian ivory is not so highly esteemed, and mammoth ivory is so uncertain in its degree of preservation that it does not find a ready sale, even though some samples almost attain the quality of recent ivory.

Even in Africa, though there is only one species of elephant, the quality of the ivory varies, that from the West Coast being harder and more translucent, that from the East Coast softer, whiter, and more opaque. The further from the Equator, the higher and drier the locality, the coarser the quality of the ivory, the best coming from the low and wet neighbourhood of the Gaboon.

The trade in ivory is quite an important one, the Board of Trade returns for 1879 giving 9,414 cwts., of the value of £406,927, as the quantity brought to this country. This meant the destruction of at least 9,000 elephants.

The best of mammoth ivory, which has been preserved by the low temperature from any change, so that it is hardly distinguishable from recent ivory, has long been an article of commerce, perhaps even from the time of Pliny.

Nordenskiöld mentions that the dredge often brought up portions of tusks, and the natives offered at times very fine tusks for sale. It is estimated that 100 pairs annually come thus into the market, and this is probably less than the real number. He travelled up the Yenesei in 1875 on board a steamer which carried over 100 tusks, of which, however, a large number were so blackened and damaged, that it was difficult to suppose them marketable.

The nearer one gets to the Polar coasts the more abundant are the mammoth remains, especially where there have been great landslips, though the tusks found at the lowest latitudes are said to be smaller. In the new Siberian Islands, in the space of a verst, Nordenskiöld saw ten tusks sticking out of the ground, and from a single sandbank ivory collectors have for eighty years reaped a harvest.

In England, dealers in ivory all seem to deny ever using mammoth ivory, though the finest specimens require the eye of an expert to distinguish them from recent ivory when cut up, and the denial must be taken *cum grano salis.*

One of the largest firms in Germany states that of imported mammoth ivory about 30 per cent. of the tusks are good and the remaining 70 per cent. worthless.

When visiting the dock warehouses in 1899 the author found about 130 tons of African and Indian tusks, and about 10 tons of mammoth ivory, and was told that the price of the former, according to quality, ranged from 10*s.* to 20*s.* per lb., whilst the best mammoth tusks rarely fetched more than 5*s.* per lb. At that time hippopotamus teeth were worth 1*s.* to 2*s.* 6*d.* per lb.; wart-hog teeth, 1*s.* to 1*s.* 6*d.*; walrus, 2*s.* to 3*s.*; and sperm whale teeth, 2*s.* to 3*s.*

In former days raiding expeditions in the Khartoum district sometimes brought back £4,000 worth of ivory, and one has been known to realise £9,200. Owing to the high value of ivory, it is cut up with thin saws, and the greatest possible care exercised to cut it with the least waste; every scrap is utilised. Billiard balls ought to be cut from small tusks, not greatly exceeding the diameter of the ball; in this way, the structure is as far as possible symmetrical about the centre of the ball, for ivory shrinks both in its length and in its width, the shrinkage being greater in the width.

The ivory throne of Solomon and the statues of ivory and of ivory and gold, mentioned in ancient writings, were probably largely composed of wood veneered with ivory.

On breaking ivory across, the fractured surface presents parallel troughs and ridges, so that the amount of tissue broken through is much larger than it otherwise would be; this obviously adds to its strength, and is a result of the peculiar disposition of its much spirally twisted dentinal tubes; this may be well seen in specimens in which the tubes have been isolated.

The tusks of an elephant are implanted in long and stout sockets; for example, a tusk 7 feet 8 inches in length and 22 inches in diameter was implanted for a length of 31 inches. They grow from persistent pulps throughout the lifetime of the animal, the last axial remains of the pulp being converted into a dentine, in which a few vascular canals may persist; this, of course, occupies the centre of the tusk and should be very small in amount.

In the Indian elephant about one half of the length of the tusk is implanted, and in young animals the pulp cavity extends beyond the implanted portion, but in older animals it does not extend nearly so far. Thus in one very big tusk the pulp cavity was a cup-shaped depression only 5½ inches deep, so that the tusk was virtually solid throughout. A knowledge of its extent is necessary, seeing that the tusks of captive elephants have to be shortened from time to time; this operation is done frequently by some, by others only at long intervals, such as ten years, in which case a large and valuable segment of ivory is cut off, and the end of the tusk then bound with metal to prevent it from splitting.

An elephant makes use of his tusks for all sorts of purposes; thus, when a tamed one is given a rope to pull, he will, by way of getting a good purchase upon it, pass it over one tusk and grasp it between his molar teeth. One tusk is usually more worn and more chipped than the other, as though much more used by its possessor. An appearance of polished spiral grooves is not uncommon on the surface of tusks; they are called rope cuts, as they are such as the wear of a rope might cause; but as they are met with on the tusks of wild African elephants also, it is not known how they are caused.

Tusks sometimes exemplify on a large scale the results of injury to the growing pulp, as it is of no infrequent occurrence that elephants, which have been shot at or otherwise wounded, escape. The thin walls of the tusk near to its open end do not offer very much resistance to the entrance of a bullet; the result of such an injury is not, as might have been expected, the death of the pulp, but in some cases abscess cavities become formed in the neighbourhood of the injury, while in others less disturbance is set up, the bullet becoming enclosed in a thin shell of secondary dentine, or sometimes lying loose in an irregular cavity, and round this the normal "ivory" is deposited; upon the outside of the tusk no indication of anything unusual is to be seen, so that the bullets thus enclosed are found by ivory turners only when sawing up the tusk for use. As the tusk grows that which was once in the pulp cavity and within the alveolus comes to be at a distance from the head, and in the midst of solid ivory.

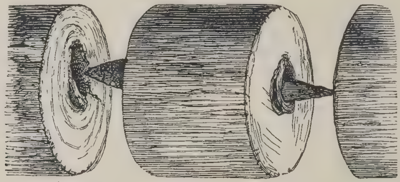

FIG. 296.—Iron spear-head, irremovably fixed in the interior of a tusk, believed to be from an African elephant. From a specimen formerly in the possession of Mr. Bennett.

As an example of the extent of injury from which a tooth pulp is capable of recovery may be cited a specimen now deposited in the Museum of the Royal College of Surgeons by Mr. Bennett, to whom the author is indebted for permission to figure it.

It is to be presumed that a trap was set with a heavily loaded spear, or that it was dropped by a native from a tree, with the intention of its entering the brain of the animal as it was going to water, both of these methods of killing elephants being practised in Africa. Sometimes as many as 100 natives are posted in trees and armed with loaded spears, the elephants being driven under the trees by others. But in this case the spear penetrated the open base of the growing tusk, which looks almost vertically upwards (see Fig. 296), and then the iron point appears to have broken off. This did not destroy the pulp, but the tooth continued to grow, and the iron point, measuring no less than $7\frac{1}{2}$ by $1\frac{1}{2}$ inches, became so completely enclosed that there was nothing upon the exterior of the tusk to indicate its presence.

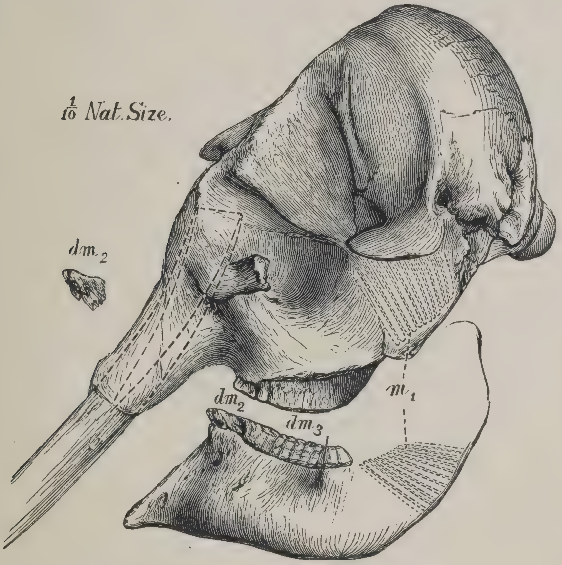

Fig. 297.—Side view of skull of young Indian elephant. The teeth in use are the second and third of the molars, which displace one another from behind forwards; the anterior of these, corresponding to a milk molar in other animals, is nearly worn out; the residual fragment is separately represented on the left. The tusk, of which only a short piece can be shown, is indicated within the socket by dotted lines, by which also the form of the pulp cavity is mapped out.

The author has been told by Mr. Erxleben that he is acquainted with another instance in which a spear-head has become completely enveloped in ivory. There are also other specimens extant, of which an excellent example is a javelin-head quite solidly imbedded in the ivory, which is also in the Museum of the Royal College of Surgeons.

Six molar teeth are developed on each side of the jaw by the elephant, and arguing from analogy, they are sometimes classified thus: milk molars $\frac{3}{3}$, true molars $\frac{3}{3}$; occasionally a rudimentary tooth in front brings up the number to seven on each side. But the peculiarity of their mode of succession renders such a classification merely arbitrary so far as the elephant itself is concerned, and it formerly depended upon analogy with the teeth of the *mastodon.* Though the elephant has, during the course of its life, twenty-four molars, they are not all in place, nor indeed are they all actually in existence at the same time. Only one whole tooth on each side, or portions of two (when the front one of the two is nearly worn out), are in use at the same time. After a tooth has been in use for some time, and is worn away, a new tooth comes up to take its place from behind it, and, absorption in the old tooth being set up, it is shed, and the new tooth pushes forward into its place (see Fig. 297). Each successive tooth is of greater size than its predecessors ; thus in the Indian elephant the first tooth has, on an average, four transverse plates, the second eight, the third twelve, the fourth twelve, the fifth sixteen, the sixth from twenty-four to twenty-seven. In the African elephant, in which the individual plates are much broader, they are fewer in number.

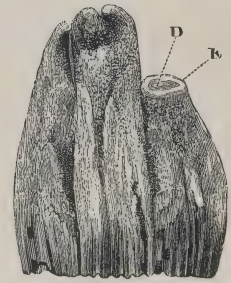

Fig. 298.—Isolated plate (= exaggerated cusp) of an elephant's tooth prior to its coalescence with neighbouring plates. At the top are seen its terminal mammillated processes, one of which has been cut off to show the central area of dentine, surrounded by enamel ; at the base would be the open pulp cavity, not shown in the figure.

A reference to the accompanying figure will indicate how the succession takes place. The tooth in reserve occupies a position at an angle to that in use ; as it moves forwards and (in the upper jaw) downwards, its track forms almost the segment of a circle. Thus its anterior corner is the first to come into use, at a time when the position of the whole tooth is still exceedingly oblique, and the greater part of it is still within the socket.

The teeth, as first formed, consist of detached plates of dentine coated with enamel, the tops of which are mammillated. These areas of dentine only coalesce after a considerable portion of their depth has been formed, and that portion of the tooth has been reached in which there is a common pulp cavity ; here dentine is continuous from end to end of the tooth.

Just as the cusps of a human molar are separate when first calcified, so these exaggerated cusps or plates of an elephant's tooth are separate from one another till a great part of their length is completed, and they only coalesce when they reach the level of the common pulp chamber; in point of fact, the elephant's tooth is mainly made up of its cusps, filled up solidly with cementum, the remaining portion being insignificant.

Several of these detached plates, such as the one shown in Fig. 298, are to be found at the back of the largest teeth even at a time when the front corner has been erupted and has come into wear.

That the tooth is thus being built up only as it is required is of obvious advantage to the animal in diminishing the weight to be carried, and in economising space.

The teeth when they begin to be erupted do not at once come into use over their whole surface, but they come forward in an oblique position, so that the front corner of the tooth has been in use for some time, and its plates have been considerably worn down, before the back of the tooth has become exposed at all. Nay, more, in the case of the larger molars the front of the tooth is actually in use at a time when its back is not yet completed. And inasmuch as the tooth comes up not vertically but obliquely, and its anterior corner is first presented to wear, it follows that the whole of the tooth gets actually worn away, with the exception of a small fragment of its posterior buried corner, which is cast off.

Had the tooth been erupted vertically, like other teeth, there would have been a comparatively large residue of implanted portion along its whole length to be cast off, so that its obliquity leads to a great economy of material.

Proboscideans formerly existed in which this peculiar succession from behind was to be found at the same time that the ordinary vertical succession was not quite lost, and amongst these creatures (the mastodons) one is able to say with certainty which of the teeth are milk molars, which are premolars, and which are true molars. And mastodons pass by insensible gradations into the elephants, so that the line of demarcation between the two genera is an arbitrary one as far as the dental characters are concerned. Other ancestral forms to be presently alluded to have been lately discovered in Egypt.

[According to the "Dimer theory" of Bolk, the teeth of the Proboscidea are polymerous, each lamella representing a tooth generation, the anterior lamella being the oldest and the posterior the youngest, the whole tooth representing a "tooth family."

This peculiarity, together with the mode of tooth replacement, is due, according to Bolk, to a curious rotation of the tooth-germ in the fœtal jaw (⁶).

The conclusions have, however, been subjected to adverse criticism by Adloff (¹), chiefly on theoretical grounds.]

Mastodon.—In the later Tertiary periods this genus, approximating in its dental and other characters to the true elephant, was widely distributed over the world. The dental formula

$$\text{i}\,\frac{1}{1}\ \text{c}\,\frac{0}{0}\ \text{pm}\,\frac{2}{2}\ \text{milk molars}\,\frac{3}{3}\ \text{m}\,\frac{3}{3}$$

is not quite the same for all members of the genus, for in some (*M. americanus*) no premolars existed.

The upper incisors formed nearly straight tusks, seven or eight feet in length ; the lower incisors also grew out horizontally from the front of the jaw, but in some species the lower tusks are rudimentary, are lost early, or are altogether absent, thus more nearly approaching to the condition met with in the elephant.

The several molar teeth of the *Mastodon* increased in size from before backwards. The crowns were built up of deep and strongly pronounced transverse ridges, of which the last molar had the largest number. The apices of the ridges, before being at all worn, were divided up into several blunt nipple-like (mastoid) processes upon which the enamel was thick and dense, but the cementum was thin, so that the interspaces of the processes were not filled up to the same level by the latter tissue, as in the elephant.

Very definite roots were formed to the molars, the wearing down of the teeth being met by the worn teeth being shed altogether from the front of the series, whilst new teeth were added to the back. Thus, just as in the elephant, the whole number of teeth were not in place at one time. Not more than three were in use at one time, and by the time the last and largest molar was cut there was but one tooth remaining in front of it, and even this was soon lost, the dentition being thus reduced to a single molar on each side.

As the succession of the molars in the *Mastodon* affords a clue to the nature of the grinders of the elephant, it is necessary to add a few words about it. Some mastodons had three milk molars, of which the last two were vertically displaced by premolars, just as in most other mammals, but the first milk molar was not so replaced (*Mastodon angustidens*). There appear to have been mastodons in which no vertical succession at all took place, *i.e.*, in which there were no premolars, and others in which there was but one.

No doubt can be entertained as to the homologies of the teeth, even in those mastodons which are not known to have any vertical succession, because analogy with those other species in which the second and third molars, counted from the front, were vertically displaced by nearly functionless premolars, tells us that the three front molars are milk molars. Now elephants develop six molar teeth on each side ; the elephant is in the same case, as to its molars, as the *Mastodon ohioticus*, which had no vertical succession, so that we thus know the elephant's grinders to be—

$$\text{dm}\,\frac{3}{3}\ \text{m}\,\frac{3}{3}.$$

Dr. Falconer mentions an elephant from the Sewalik Hills (*E. planifrons*) in which two rudimentary premolars, of no functional importance, actually existed, and so the determination of the elephant's working teeth as—

$$\mathrm{dm}\,\frac{3}{3}\ \mathrm{m}\,\frac{3}{3}$$

rests not only upon analogy, but upon actual observation.

[**Palæomastodon.**—The teeth of this genus have been described by Andrews (5), and the knowledge available summarised in the "Catalogue of the Tertiary Vertebrates of the Fayûm" (1906). In the spring of that year further specimens were obtained by which he was enabled to give an account of the milk dentition. The tusks of the upper jaw (i^2) are strongly compressed laterally with a sharp posterior edge. They curved downwards and outwards with a slight spiral twist, terminating in a sharp point. The roots of these teeth extend backwards as far as the level of pm^2.

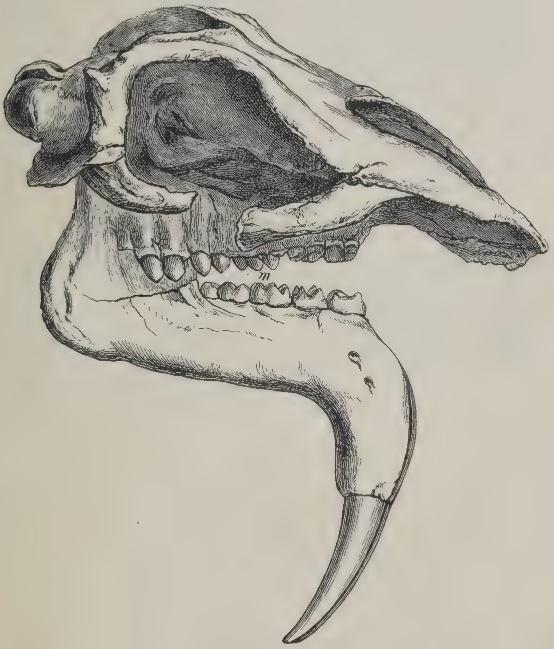

FIG. 299.—Skull of *Dinotherium*. (After Owen.)

The corresponding lower incisors are long and procumbent, the outer border being convex and serrated. They grow from persistent pulps, and Andrews thinks it possible that they are permanently growing milk teeth.

The maxillary anterior milk molar (mm^2) consists of a large laterally compressed cone with a small accessory tubercle on its posterior edge. The cingulum is well marked. Mm3 is bilophodont, and mm4 trilophodont.

The anterior mandibular milk molar (mm2) consists of a large median cone with a smaller cusp anteriorly, and another posteriorly. It is two-rooted. Mm2 has two pairs of transversely arranged cones, the external one of each pair being the larger, a small accessory tubercle filling the valley between them. Anteriorly to these pairs of cusps is a larger one connected with the antero-external cone; posteriorly is a sort of talon.

Mm3 is two-rooted, and is an extraordinarily elongated tooth of a trilophodont pattern, as is also the first true molar.]

Dinotherium, a large animal, not unlike the Sirenia in the character of its cranium, and, like them, probably of aquatic habits, was remarkable for possessing large tusks in its lower jaw, by analogy known to be incisors, none being present in the upper jaw. The tusks projected downwards at right angles with the body of the jaw, and were curved backwards. The portion of the jaw about the symphysis was deflected downwards, so as to afford an adequate implantation for these anomalous tusks. The dentine of these tusks does not, however, present the characteristic ivory pattern.

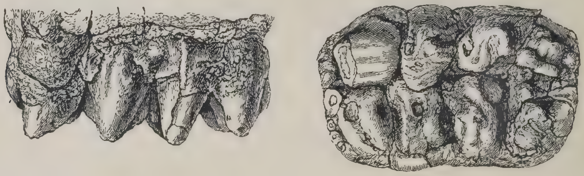

Fig. 300.—Molar tooth of *Mastodon*.

Dinotherium was as large as an elephant, and the downward pointing tusks were about 2 feet in length; as, however, tusks of only half this length were found in some jaws of identical dimensions and in other respects similar, it is believed that the male *Dinotherium* had larger tusks than the female. The molar teeth were much like those of a tapir—

$$i\,\frac{0}{1}\;c\,\frac{0}{0}\;pm\,\frac{2}{2}\;m\,\frac{3}{3}.$$

The succession was vertical, as in other mammals, and it had dm $\frac{3}{3}$.

But *Dinotherium*, *Mastodon*, and *Elephas* present a very instructive series of modifications in which we see how the excessively complex grinder of the Indian elephant was attained by degrees.

The molar of *Dinotherium* somewhat resembles that of a tapir; it has not any very great exaggeration of its cusps, and does not deviate very widely from the form of many other mammalian teeth; the premolars and molars all have two ridges, with the exception of the last milk molar and the first true molar, which have three.

The similarity in pattern between the last deciduous premolar and the first true molar, previously referred in the case of many other forms recent and fossil, may be seen in Fig. 300. The explanation, viz., that the last dpm is really the first of the true molar series, is probably true in the case of the elephant also.

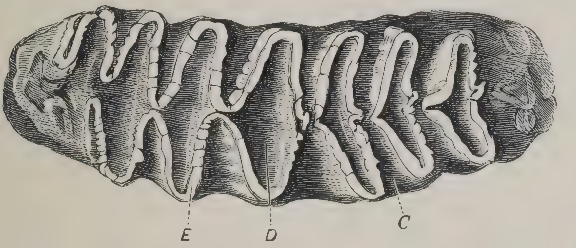

Fig. 301.—Molar of African elephant. *E*. Enamel. *D*. Dentine. *C*. Cementum.

The tooth of *Mastodon* has its cusps or ridges more numerous and more pronounced, as is seen in the accompanying figure (Fig. 300).

Other mastodons have more numerous ridges upon the teeth, and the African elephant has as many as ten upon its last or largest molar, although in it the ridges are individually wide and strongly pronounced.

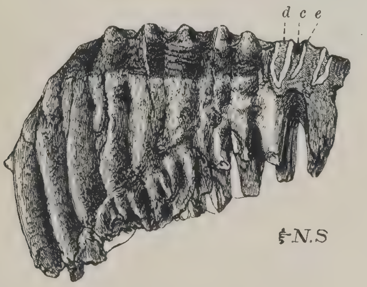

Fig. 302.—Molar tooth of African elephant, showing the form of its roots, &c. *d*. Dentine. *c*. Cementum. *e*. Enamel.

In the Indian elephant the ridges or plates are still more numerous, the roots very inconspicuous, and the whole formed into a solid block by cementum.

The gradual increase in complexity in the "ridge formula" (or number of ridges in each tooth) of the molars is well seen in the following table, from Flower's Hunterian lecture (*Nature*, March 2, 1876); it is a corrected table taken from Dr. Falconer's "Palæontological Memoirs."

	Milk Molars.			True Molars.			Total.
	I.	II.	III.	I.	II.	III.	
Dinotherium giganteum	1	2	3	3	2	2	13
Mastodon (Trilophodon) americanus	1	2	3	3	3	4	16
,, (Tetralophodon) arvernensis	2	3	4	4	4	5	22
,, (Pentalophodon) sivalensis	3	4	5	5	5	6	28
Elephas (Stegodon) insignis	2	5	7	7	8	10	39
,, (Loxodon) africanus	3	6	7	7	8	10	41
,, ,, meridionalis	3	6	8	8	9	12	46
,, (Euelephas) antiquus	3	6	10	10	12	16	57
,, ,, primigenius	4	8	12	12	16	24	76
,, ,, indicus	4	8	12	12	16	24	76

Some variability exists in the number of ridges, especially when they are very numerous, but the above may be taken as averages: and some species intermediate in the "ridge formula" have been since discovered; thus M. Pentelici and M. Andium bridge the distinction between *Trilophodon* and *Tetralophodon*, and *Elephas melitensis* comes between *Loxodon* and *Euelephas* (Flower).

It remains to describe, somewhat more in detail, the structure of an elephant's tooth, and this has been deferred till the last, because it can be the more easily understood when the manner of its origin has been mastered. In the *Mastodon* the molar consists of a crown with strong cusps standing apart, and with marked roots; in the African elephant that part which consists of cusps has become the greater bulk of the tooth, the roots are comparatively insignificant, and the interspaces of the cusps are filled up with cementum. The molar of an Indian elephant consists of a larger number of yet more elongated and flattened cusps, so that the greater part of the tooth is made up of these flattened plates, fused together with cementum, and so forming a strong and solid mass; the roots are comparatively inconspicuous. Thus we have a process of evolution going on exactly as in other Ungulata: the rooted and distinctly cuspid tooth of the *Mastodon* has but little coronal cement, whilst as the cusps and ridges deepen, and the tooth becomes more of hypsodont type, at the same

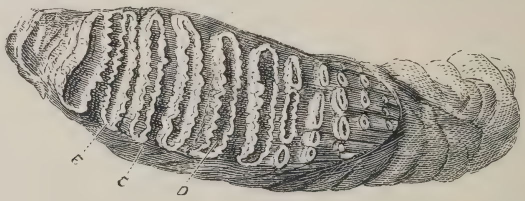

FIG. 303.—Molar tooth of an Asiatic elephant, showing the transverse plates of dentine bordered by enamel.

time the ridges become more numerous, and the coronal cement increases in quantity so as to fuse it into a solid block.

When the tooth is a little worn each plate consists of an area of dentine surrounded by enamel. The interspaces of the series of plates are wholly filled up by cementum ; the summits of each plate were originally mammillated, and divided up into more numerous blunt processes than the corresponding parts of the tooth of a *Mastodon ;* so when the tooth comes into use the rounded tips are soon worn off, and the grinding surface of the tooth then consists of narrow transverse bands of dentine, surrounded by enamel, and of cementum in their interspaces. The difference in hardness between these three tissues preserves a constant rough surface, owing to their unequal rate of wear. In their wild condition elephants eat trees with succulent juicy stems, and oftentimes grass torn up by the roots, from which they roughly shake out the adherent earth. In confinement, the food containing less that is gritty, the teeth become polished by working against one another, but the rate of wear is insufficient to keep their surfaces rough ; for the softer cementum does not get worn down in the interspaces of the plates of dentine and enamel, but remains on a level with them.

The celebrated elephant "Jumbo" suffered from insufficient wear of his teeth, so that the earlier ones, being insufficiently worn, were not got rid of at the proper time, and interfered with the normal development of their successors.

The recent Proboscidea being so very divergent from the usual types of mammalian dentition, especial interest attaches to the discovery in Egypt of ancestral forms in Eocene formations, and therefore long antecedent to the appearance of well-marked Proboscidea (3). *Mœritherium* presented a full set of teeth ; of the incisors, the second was greatly enlarged and the canine dwarfed ; all six of the cheek teeth were in use at once. The molars were brachyodont and bilophodont (quadritubercular). The process of evolution proceeded from this form along the following lines : the facial region shortened and the premaxillæ widened, the mandible at the same time becoming short and stout and the symphysis massive. From appearances at this stage it is probable that the upper lip and nares were prolonged so as to resemble the beginnings of a proboscis.

The upper first and third incisors dwindled and were lost, the second greatly increasing, so that there now remains no doubt but that the great tusk of the elephant is its second incisor ; the canines were soon lost altogether. In the earlier forms there was a vertical succession of the anterior cheek teeth, but in the later forms no succession is to be detected. In the lower jaw the second incisor persisted long as a functional tooth, and this is the tooth which was retained as a lower tusk in the *Mastodon.* And finally the steps by which the brachyodont quadritubercular molars of *Mœritherium* were transformed into the hypsodont proboscidean type are illustrated in this Egyptian series (2).

In *Mœritherium* all three pairs of upper incisors were present, though the first and third pairs were quite small and the second pair were long trihedral tusks, growing from persistent pulps and directed nearly vertically downwards. Small canines were present.

In *Palœomastodon* (Andrews) the first and third pairs of upper incisors have disappeared, and the second formed longer tusks directed forwards and downwards, which carried a band of enamel on their outer surfaces. No canines were present.

In *Tetrabelodon* (sometimes called *Mastodon angustidens*) the general contour of the skull was approaching that of an elephant, though the mandible was long and slender. The upper tusks had now attained to a length equal to the rest of the skull, and were directed forwards, with a slight downward curve ; the band of enamel still persisted on their outer faces.

In *Mastodon* the skull had the form of an elephant's skull, the mandible had become more massive, and the lower tusks had often disappeared. The upper tusk was far longer than the skull, had assumed an upward curvature, and had lost its enamel band.

The bunodont or lophodont cheek teeth were all in use at one time in *Mœritherium* and *Tetrabelodon*, but in *Palœomastodon* the front members of the series were shed, so that in many specimens only the two last molars remain.

Thus by a fairly gradual series of transitions we are led from the middle Eocene *Mœritherium*, a creature not strikingly aberrant, to the very highly specialised recent elephants. It is pointed out that in the peculiar succession of teeth from behind forwards (see p. 597), as well as in characters not related to the teeth, the Proboscidea have resemblances to the Sirenia (^{3}).

[Dr. Andrews thus summarises (^{5}) "the changes which the dentition of the *Elephantidœ* has undergone in passing from *Mœritherium*, in which three permanently functional premolars are present in both jaws, to the recent elephants in which these teeth have been completely lost. In *Mœritherium*, the most primitive form yet found, unfortunately the milk dentition is very imperfectly known, the only specimen showing it being an imperfect mandibular ramus, in which the molariform last milk molar is about to be replaced by a simple premolar. Nevertheless, although all the milk teeth have not been directly observed, the presence of three premolars in each jaw in the permanent dentition makes it fairly certain that at least as many milk molars were present in the young. In this genus, even the last premolar is not molariform, although the last milk molar is already bilophodont, with a well-developed rudiment of a third ridge. In *Palœomastodon* there are three milk molars in each jaw, but here one of the premolars present in *Mœritherium*, viz., the second in the lower jaw, has been lost, and the posterior premolars have become bilophodont, but they still remain simpler than the molars in which a third ridge has been acquired. The posterior milk molars have likewise become trilophodont, and it is the rule that the posterior milk teeth in this group increase in complexity of crown structure in the same way as the true molars, although in the genus *Elephas* even the last milk molar in almost every case has fewer ridges than the molar behind it. In the latest types, like *E. primigenius*, in which the molars attain the maximum degree of complication, the milk molars likewise reach their highest development; thus, in *E. primigenius*, the last milk molar may have as many as twelve transverse crests.

"In *Palæomastodon*, all the premolars and molars remain in use simultaneously till the end of the animal's life, and the most significant character noticeable in the molars, seen in the light of the subsequent history of the dentition, is the sudden enlargement of m2 and m3 compared to m1, for it is mainly in consequence of the increase in the size of the posterior molars that the peculiar characters of the dentition of the later Proboscidea arise. It is also interesting to note that, behind the last molar, large sinuses are present in the maxilla, almost as if in preparation for the further enlargement of that tooth; probably in part, at least, it is due to the presence of these sinuses that this further increase in size is possible.

"In the next stage of which anything is known, that is to say, in *Tetrabelodon angustidens*, a considerable advance is observable. In this species also there are three milk molars in each jaw, all being replaced by premolars in the upper jaw, the posterior two only in the lower, but although these premolars are cut and remain functional for a longer or shorter time, nevertheless the increase in size of the second, and especially of the third, molar is so great that, not being accompanied by any corresponding increase in the length of the portion of the jaws in which the cheek teeth are situated, there is not sufficient room for the whole series to be in position at the same time. As the posterior molars come into use they move forwards in the jaw, so that the anterior teeth are, one after another, thrust out and shed till, in the adult, only the two posterior molars remain in use on each side of the upper and lower jaws, and even in this early type probably the second molars also are shed in advanced age, so that finally only the enlarged third molars continue functional. The further history of the premolars is one of gradual suppression. Thus in *Tetrabelodon longirostris* according to Röse only one of the milk teeth on each side is ever replaced by a premolar, and this is not the last, but the last but one, which is cut when the first molar germ still lies in the jaw, and the crown of the second is not yet calcified.

"In this case, however, it seems probable that the last premolar has escaped notice, since it is known to be present in later forms. For instance, premolars have been observed in *Elephas* (*Stegodon*) *clifti* and *Elephas* (*Loxodon*) *planifrons*, both of which species are very probably on the direct line of descent of the modern elephants. It is noteworthy that in the otherwise more primitive mastodons, such as *M. arvernensis* and *M. americanus*, the premolars were soon lost, and that it is these forms that have died out without leaving any descendants, so that here, as is usually the case, a more conservative type (at least so far as the replacement of the milk molars is concerned) has given rise to the modern elephants, while the other forms, which, in this respect at least, became early specialised, have been swept away probably on account of a loss of power of adjustment to a further change of circumstances."]

The Teeth of the Sirenia.

SIRENIA
- *Manatidæ.*
- *Halicoridæ.*
- *Rhytinidæ.*

Probably more nearly connected with the Ungulata than with any other order, but still rather widely removed from them, stands the limited order of Sirenia, aquatic mammals formerly termed Herbivorous Cetacea, a term rather objectionable, as they are not allied to the true Cetacea.

The order is now represented by two genera only, the dugong (*Halicore*) and the manatee (*Manatus*), but a third genus (*Rhytina*) has only become extinct within about a century. Their teeth, and other points in their organisation, indicate that they are allied to the Ungulata, and perhaps to the Proboscidea, though their peculiarities are such as to elevate them to the rank of a distinct order. They are of large size and frequent shallow water, such as the mouths of great rivers, their food consisting of seaweed and aquatic plants. Their incisors and molars, when both are present, are widely separated, the former varying from being quite rudimentary to formidable tusks.

The dentition of the **Dugong** is in several respects a very interesting one; the front part of the upper jaw, consisting in the main of the intermaxillary bones, bends abruptly downwards, forming an angle with the rest of the jaw. This deflected end of the jaw carries two tusks, of each of which the greater part is buried within the bone itself. The tusk has an investment of enamel over its front and sides, but over the posterior surface of cementum only, so that in the disposition of the three structures it recalls the characteristics of a rodent incisor, like which it is worn away obliquely so as to keep a constantly sharp edge, and, like which, it grows from a persistent pulp.

In the female, the tusks (incisors) do not project from the gum, their pulp cavities are closed, and the investment of enamel is complete over the whole top of the tooth.

The sloping surface of the upper jaw is opposed by the region of the symphysis of the lower jaw, which is of unusual depth. In this deflected part of the lower jaw there are eight or ten (four or five on each side) shallow and rather irregularly shaped sockets, in which curved distorted teeth may be found in a fresh specimen, but it must not be too aged an animal, as they eventually become removed by a process of absorption.

These abortive teeth are excellent examples of vestigial teeth, as not only are they stunted, and even ultimately removed by absorption, but they are actually covered in by dense horny plates, which clothe this part of the jaw, and so the teeth become absolutely functionless.

These horny plates, in their structure analogous to whalebone, are possessed also by the manatee and *Rhytina*. On the free surface they are beset with stiff bristles, and are throughout built up of hair-like bodies welded together by epithelium.

Behind the region covered in by the horny plates, the dugong has five molar teeth on each side, of simple form, like those of the Edentata, and consisting of dentine and cementum only. Their form is cylindrical, with the exception of the last, which is laterally grooved, but before they are worn they have tuberculated crowns, and are of semi-persistent growth; thus they are evidently degenerating teeth, and in *Rhytina* they had wholly disappeared.

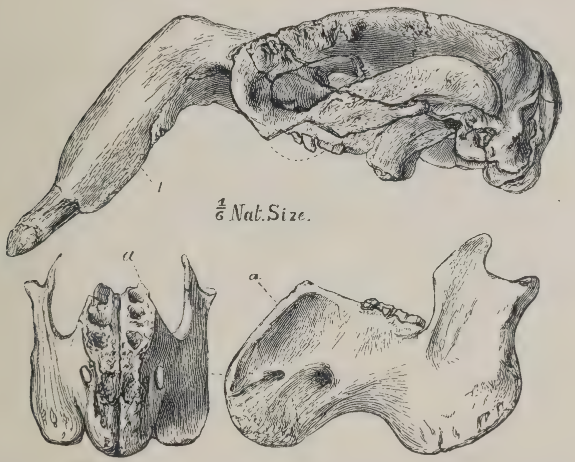

FIG. 304.—Side view of cranium and lower jaw of a dugong (*Halicore indicus*). From a specimen in the Museum of the Royal College of Surgeons. The surface of the deflected portion of the lower jaw, with its sockets for rudimentary teeth, shown both in front and in profile view, is indicated by the letter *a*, the corresponding surface of the upper jaw by the letter *b*.

By the time the last molar is ready to come into place the first of the series is being removed by absorption of its root and of its socket. In aged specimens only two molars remain on each side of the jaws.

The dugong is also peculiar as having a single deciduous tooth, namely, a predecessor to the incisive tusks; but it has been doubted whether it be not rather a vestigial incisor than a milk tooth.

The molar teeth of the dugong consist of a central axis of vaso-dentine, a much larger mass of ordinary unvascular dentine, and a thick layer of cementum, but they do not share the peculiarities of the manatee's tooth.

[Kükenthal has recently published an account of the development of the teeth in the dugong (⁹). This, he states, confirms the conclusions at which he had previously arrived, when investigating the tooth-genesis in the manatee (⁸), as to the fusion of enamel-organs. He claims to have found evidence of the lateral fusion of lacteal and prelacteal enamel-organs in the premolar region of the lower jaw.

In the molar region, the entire remains of the dental lamina are used up in the formation of the enamel-organ of the functional tooth, which not only explains the absence of replacing teeth in this situation, but also tends to confirm the view, held by many, that molar teeth belong to the successional series. Large cyst-like epithelial nodules, similar to those figured by Marett Tims and others (cf. p. 371), are present in regular order rather in front of the teeth " anlagen " and situated to the labial side of the enamel ridge. If these are aborted tooth-germs, which is probable, then, according to Kükenthal's interpretation, they represent a vestigial dentition antecedent to the prelacteal. If this be the case, it supports Röse's statement as to the presence of a similar dentition in man. This would bring up the total number of dentitions in the Mammalia generally to five.*]

In the **Manatee,** just as in the dugong, the front portion of the jaws is depressed and is covered in by a horny plate.

The manatee has $i\,\frac{2}{2}$, but they are rudimentary, and are buried under the horny plates which occupy the front of the mouth, and there are no canines. Gervais (⁷) gives a larger number of rudimentary teeth, indeed as many as twelve.

And Kükenthal (⁸) says that the rudiments which still exist show that the ancestors of the manatee had three incisors—a canine and three premolars on each side in the lower jaw, but in the upper jaw reduction has gone yet further. He has found a milk dentition consisting of $i\,\frac{3}{3}$, $c\,\frac{0}{1}$ dpm $\frac{0}{3}$.

The molar teeth of the manatee are much more numerous and more complex in form than those of the dugong, and they approach to the configuration of the teeth of the tapir very closely.

The manatee has been said to have as many as forty-four molars, which are not, however, all in place at one time, the anterior being shed before the posterior are come into place. No vertical succession is known to take place amongst them.

It has long been known that teeth are shed off from the front of the series before the eruption of the hindmost tooth, so that, though the creature develop at least forty-four molars, there are seldom more than six in place at one time on each side.

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* The evidence furnished in the paper to which reference is made does not appear to me to be conclusive.—H. W. M. T.

But Oldfield Thomas (12) has described a yet more remarkable and, indeed, unique succession of teeth. By comparing the jaws of manatees of various ages it is found that the teeth for a long time continue to increase in size, so that it is possible to more or less exactly identify the corresponding teeth in various specimens, although they have come to occupy different places in their order in the row, owing to the shedding of teeth from the front of the series.

Compared in this way, the jaws of individuals of different ages give evidence of the development of at least twenty molar teeth on each side of each jaw, whilst in the very oldest specimen available there was still always a tooth in reserve at the base of the coronoid process.

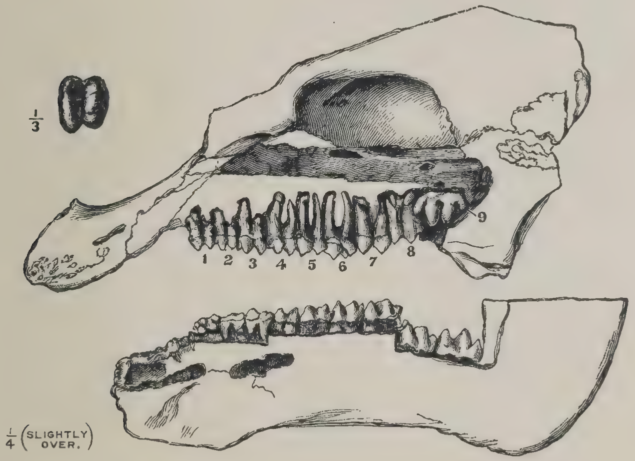

Fig. 305.—Upper and lower jaws of the manatee. In the upper jaw the bone has been removed so as to show the roots of the teeth and the absorption of the roots of the anterior members of the series, as also the reserve teeth. In the lower jaw some bone has been removed in the front and at the back, but over the four middle teeth it is untouched. The bilophodont crown is shown separately.

It seems impossible to resist the conclusion that the whole row of teeth is undergoing a perpetual migration forwards. Whilst the outer shell of the jaw is very dense, the alveolar septa are very porous; and it would thus seem easy for the alveolar septa to be removed whilst the teeth move forward, guided by the unaltered bony walls on either side.

The alveoli themselves are in some respects unlike those of most mammals.

In the central portion of the lower jaw figured, some of the bone has been cut away to expose the roots or the unerupted teeth. It will be noticed that the bone presents a perfectly level top, and that it is not continued up in tongues between the teeth so as to closely embrace their necks, but the bifurcation of the roots is visible. If the teeth were away, the surface of the jaw would be a flat area, a good deal wider than the width of the teeth, with holes in it where the roots had lain.

In one specimen there were nine molars on each side, and behind these are two more which are not yet erupted. The roots of the foremost three teeth are considerably absorbed, those of the front tooth having been almost completely removed, though in each tooth the posterior root is more attacked than the anterior. The development of the bone of the socket has curiously followed up the absorption, so that, notwithstanding the removal of considerable portions of the roots, no vacant space is left below them.

In *Phacochœrus* (the African wart-hog) the anterior cheek teeth are shed, and their roots show evidence of absorption, but in the elephant little absorption takes place except in the earlier molar teeth, the later ones being completely worn away. In the elephant the molar teeth increase enormously in size from before backwards by the addition of extra plates. In the manatee the teeth increase in size very gradually, and an indefinite number are formed. There is thus a partial parallel between the two. (Cf. Proboscidea.)

It has been mentioned that the teeth of the manatee are tapiroid in external form; they also possess peculiarities in minute structure, which are unusual in mammalian teeth. In examining some teeth, dentine, to all intents and purposes of the hard unvascular variety, was permeated by a system of larger, or "vascular," canals, which were arranged with much regularity, and were most abundant near to the periphery of the dentine, where they communicated with one another. The dentinal tubes did not radiate from these vascular canals; they, so to speak, take no notice of them, so that there is an ordinary unvascular dentine with a system of channels, which are no longer pervious, having become obliterated and presenting the appearance of greatly elongated interglobular spaces. (See p. 102.)

The enamel of the manatee is also remarkable for the absolute straightness of its enamel prisms in many parts of the tooth.

This animal has a curious manner of feeding: the halves of the upper lip, deeply cleft in the middle, are beset with short stiff bristles, and are used to tuck food into the mouth; when these fail the flappers are raised and used to assist.

The huge extinct **Rhytina,** a little more than a century ago abundant in Behring's Straits, was altogether without teeth, but was furnished with dense, strongly ridged, horny plates.

The Sirenia were abundant in Miocene and Pliocene seas. *Halitherium* had molars somewhat like the manatee, but had tusk-like incisors in the upper jaw. The front of the upper and lower jaws was deflected, as in the dugong and manatee. The anterior premolars were small, simple, and cylindrical, and the molars more complex, and there was probably a vertical succession in the premolar region.

Prorastomus, a Tertiary fossil form only known by the skull, was yet more generalised, and had a tapir-like dentition i $\frac{3}{3}$ c $\frac{1}{1}$ pm $\frac{4}{4}$ or pm $\frac{5}{5}$ m $\frac{3}{3}$, and serves to link the Sirenia yet more closely with terrestrial mammals.

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CHAPTER XX.

THE TEETH OF PRIMATES.

- PRIMATES
  - Prosimiæ
    - *Tarsiidæ*
    - *Lemuridæ*
  - Simiæ
    - Platyrrhina
      - *Hapalidæ*
      - *Cebidæ*
    - Catarrhina
      - *Cercopithecidæ*
      - *Hylobaditæ*
      - *Anthropomorphæ*

THE order Primates embraces man, apes, monkeys, and lemurs.

Some naturalists have been disposed to separate the *Lemuridæ* from the rest of the Primates, on the ground that some lemurs approximate rather closely to the Insectivora, while again the order Insectivora contains some forms which recall the lemurs; the lemurs are exceedingly ancient and generalised forms, being found even in the Lower Eocene, and Cope considers that they may have been the parents of many widely different mammalian forms.

But although the *Lemuridæ* are undoubtedly inferior to the monkeys, and stand apart from them more widely than do the monkeys and man, most authors now place them in the order Primates.

Prosimiæ.—[The *Tarsiidæ* are represented by the single species *Tarsius spectrum*, which is found in many of the islands of the Indo-Malayan archipelago. This animal is rather smaller than a squirrel, with very large eyes and ears and a long tufted tail. Nocturnal in habits, it feeds principally on insects, though it does eat larger animals, such as lizards. Its dental formula is $i\,\frac{2}{1}\,c\,\frac{1}{1}\,pm\,\frac{3}{3}\,m\,\frac{3}{3}$. In the upper jaw the outermost incisor is wanting; in the lower jaw the first as well as the third incisor is absent. The canines are semi-erect, and the apex of the lower canine diverges from the incisor. The lower premolars are smaller than the corresponding teeth in the upper jaw, the first lower premolar being decidedly smaller than the two posterior teeth of the series. The molars have numerous pointed cusps of an insectivorous type.]

The lemurs for the most part are found in Madagascar, and to a less extent on the mainland of Africa and in Southern Asia, though in the Tertiary Eocene period they were far more widely distributed. In their dentition, just as in other characters, they differ somewhat from the true monkeys, though, on account of there being several very aberrant in form, it is difficult to give any general account of them, the more so as their dentitions, so far as they are known, vary much more than does their food. Most lemurs eat insects, reptiles, small birds, and fruits.

Generally, the upper incisors are very small, and widely separated from one another ; these are antagonised in the lower jaw by six or eight long, thin, narrow procumbent teeth, generally regarded as being two pairs of incisors and the lower canines, though some regard them all as incisors and the lower canines as being absent ; in both upper and lower jaws the next tooth is large and pointed like a canine, but the lower caniniform tooth bites behind the upper, and so is held not to correspond to it, but to be the first premolar. In this respect they differ from the monkeys, in which the lower caniniform tooth is the same tooth as in man, but it is interesting to find that in the fossil forms this difference does not exist, so that lemurine forms may easily have been the ancestors of the monkeys proper, and hence especial interest attaches to them. The premolars are compressed from side to side, and are very sharp, while in many of them the lower premolars are two-rooted, the roots being more or less completely in the position of outer and inner, not of anterior and posterior roots. The molars are provided with long sharp cusps, which are worn down in old animals, and whilst the upper molars in many lemurs are armed with four cusps, the upper and lower molars being very generally alike, a three-cusped molar of tritubercular form is the one most typical of the group, and is general amongst the extinct species ; the latter also present some examples of the full mammalian number of four premolars, and so were, in many particulars, much less specialised than their recent descendants.

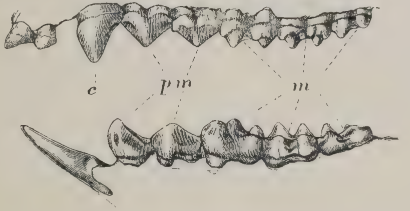

FIG. 306.—Teeth of the indris. *c.* Canine. *pm.* Premolars. *m.* Molars.

Some fossil lemurs had four molars, like the marsupials on the formula once adopted for them, and four lower molars have been seen in *Lemur fulvus*, the fourth being a counterpart of the third on a smaller scale. Howes suggested that as four molars now and then occur in the mammalia, and as supernumerary teeth often occur in the gorilla, the ancestors of the Primates may have had four molars.

The **Indris,** the largest of the lemuroids, has

$$\mathrm{i}\,\frac{2}{1}\;\mathrm{c}\,\frac{1}{1}\;\mathrm{pm}\,\frac{2}{2}\;\mathrm{m}\,\frac{3}{3},$$

$$\text{or }\mathrm{i}\,\frac{2}{2}\;\mathrm{c}\,\frac{1}{0}\;\mathrm{pm}\,\frac{2}{2}\;\mathrm{m}\,\frac{3}{3}.$$

In this animal there are fewer teeth than in the true lemurs, there being only one incisor in the lower jaw; and as the canine ranges with it, the upper canine is antagonised by a two-rooted, pointed tooth which closes behind it, and is a premolar. In the milk dentition there are two additional teeth in the fore part of the lower jaw, one apparently the true canine and the other a premolar.

The premolars are compressed and pointed, and the true molars are quadritubercular. It has been suggested by Cope that the procumbent position of the lower incisors, which do not accurately oppose the upper incisors, may have been acquired by the animal's habit of combing its fur with these teeth (⁴).

In the lemurs proper there are thirty-six teeth, their dental formula being usually written

$$i\,\frac{2}{2}\;c\,\frac{1}{1}\;p\,\frac{3}{3}\;m\,\frac{3}{3}.$$

The lower canine is procumbent, ranging with the incisors, and may perhaps be counted as a third incisor.

In some of the lemuroids the upper incisors are further reduced (*Lepidolemur* has them absent or rudimentary, and *Nycticebus* has often only one), whilst in the very aberrant aye-aye (*Cheiromys*) the incisors are enormous, so that its dentition imitates the rodents:—

$$i\,\frac{1}{1}\;c\,\frac{0}{0}\;pm\,\frac{1}{0}\;m\,\frac{3}{3}=18.$$

Cheiromys.—In both upper and lower jaws the incisors form a single pair of large curved teeth, growing from persistent pulps, and wearing obliquely, so as to constantly preserve a sharp cutting edge. The enamel is very much less thick, if not altogether absent, upon the backs of the upper incisors, but the lower incisor, which is very narrow from side to side, and very thick from back to front, is composed very largely of enamel, the dentine constituting a comparatively small part of it.

After a considerable interval, which is devoid of teeth, there follow four upper and three lower teeth, which are not of persistent growth, but have definite roots, and resemble the molars of many omnivorous rodents.

Although, functionally, its teeth are those of a rodent, yet, despite this adaptive resemblance, the milk dentition retains certain characters which indicate the lemurine origin of the creature.

In the upper jaw the milk dentition consists of two small incisors, a canine, and three molars, in the lower jaw of two small incisors and two small molars; it is said that in an early stage a third milk incisor is to be found:—

$$di\,\frac{2}{2}\;dc\,\frac{1}{0}\;dm\,\frac{2}{2}.$$

The permanent incisors push their way up between the first and second milk incisors; at a certain stage all three are to be seen at once, but the large size of the permanent incisors causes the speedy loss of the milk incisors.

No known rodent has so many well-developed milk teeth; the aye-aye thus affords an excellent example of a milk dentition preserving characters which are lost in the extremely modified adult dentition.

Being a somewhat rare and strictly nocturnal animal, little is known of its food; some have believed that it made use of its rodent incisors to cut away portions of wood in order to get at the grubs contained in it, drawing them out of their hiding place by means of its curiously elongated finger, whilst others believe that it gnaws the sugar-cane. One specimen kept in confinement had the habit, no matter what it had been eating, of passing each of its long fingers carefully through its mouth after finishing its food, as though these fingers were apt to get soiled in the getting of its natural food. But, whatever the nature of its food may be, it is certain that its scalpriform incisors are put to hard work, and so kept worn down, for in a specimen kept for a time in the Zoological Gardens, which was supplied with soft food, both upper and lower incisor teeth grew to an excessive length, and ultimately caused the animal's death by the points of the lower incisors perforating the palate. Fig. 308 represents the muzzle of this specimen, and although the upper teeth have grown to an inordinate length, and have diverged from one another, it will serve to show the rodent-like aspect of its mouth.

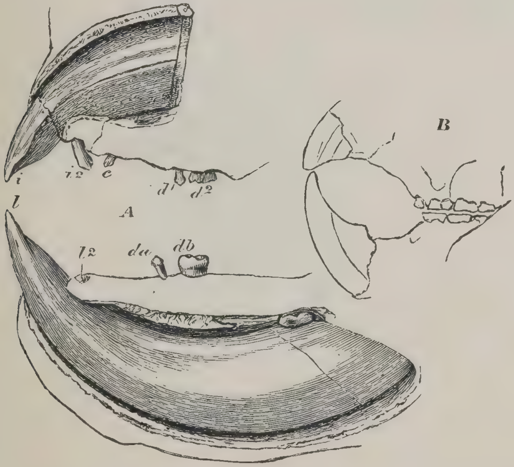

FIG. 307.—Upper and lower jaws of *Cheiromys*. A. Milk dentition, with the permanent incisors just erupting. *i*, *l*. Upper and lower permanent incisors. *i* 2, *l* 2. Upper and lower milk incisors. *c*. Milk canines. *d* 1, *d* 2, *d a*, *d b*. Upper and lower milk molars. (Twice natural size.) B. Reduced figure of permanent teeth. (After Peters.)

The special interest which attaches to the dentition of *Cheiromys* has been already alluded to; to briefly recapitulate, it is this: in Madagascar, an isolated area separated by a wide tract of deep sea from other areas, true rodents are almost absent at the present day, but lemurs abundant. But one of the lemurine animals which are to be found there has been so modified that its teeth to all intents and purposes are those of a rodent. Yet with all this modification it retains characters (notably its milk dentition) which are quite unlike those of true rodents, but which recall the manner of its origin from more generalised lemurine forms.

Simiæ.—The true monkeys are divided into two great groups, the New World monkeys and the Old World monkeys. The former differ in many respects from the latter; for the most part they have prehensile tails, and their nostrils are set somewhat widely apart, whence they are called *Platyrrhine*, or wide-nosed, monkeys, and they differ also in their dental formula, which is—

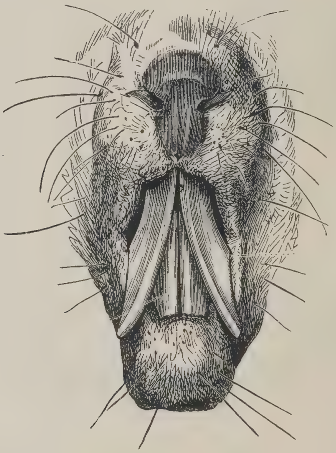

Fig. 308.—Aye-aye (*Cheiromys*), which died in the Zoological Gardens. (After Dr. Murie.) The upper incisors, from want of sufficient use, have grown long and diverged from the middle line.

$$\mathrm{i}\,\frac{2}{2}\;\mathrm{c}\,\frac{1}{1}\;\mathrm{p}\,\frac{3}{3}\;\mathrm{m}\,\frac{3}{3} = 36.$$

They are divided into *Hapalidæ* (marmosets) and *Cebidæ*.

The little **marmoset** monkeys have only thirty-two teeth, but they still agree with the other New World monkeys in having three premolars on each side, the molars having been reduced to two in number. The upper molars of some New World monkeys, notably *Ateles* and *Mycetes*, have the antero-internal and postero-external cusps joined by an oblique ridge, a character which is shared in the Old World groups by man and the anthropoid apes only.

In the *Cebidæ* the molars have very sharp cusps, as in the Insectivora, and the upper and lower molars are not alike.

In the spider monkeys (*Ateles*) the outer lower incisors are caniniform, and the canines, which are long and sharp, are very like the anterior premolars, but have their outer cusps much longer. The inner cusp of the anterior lower premolar is hardly developed, but in pm_3 the inner cusp and posterior cingulum are more pronounced, and in pm_4 the former yet more strongly expressed; they are all single-rooted, and show the relationship of the canine to the premolars excellently well.

The upper premolars, especially the last, have roots bifurcated near their tips, but have not three roots. The bifurcation in the root of pm^1 takes place only low down, in pm^2 lower still, and pm^3 is single-rooted and small, so that the teeth show a tendency to reduction.

Of the upper molars the first two are three-rooted, but the third is hardly even bifurcated.

All Quadrumana have well-developed milk dentitions.

Old World, or *Catarrhine*, monkeys all have the same dental formula as man :—

$$i\,\frac{2}{2}\;c\,\frac{1}{1}\;p\,\frac{2}{2}\;m\,\frac{3}{3} = 32.$$

They have nipple-shaped cusps to the molars, as in man and the anthropoid apes, but in the *Pithecidæ* the upper and lower molars are alike. As an example the **Macaque** monkey may be taken. The upper and lower incisors, but especially the former, are directed obliquely forwards, and the second incisors are very much smaller than the first. In the upper jaw a considerable interval separates the incisor from the canine, which is a very large tooth, somewhat triangular in section, with a sharp edge directed backwards, and with a deep groove on its anterior surface. The lower canine is a sharp and powerful tooth, though it is very much smaller than the upper.

There is considerable difference in the size of the canine in the two sexes, that of the male being very much the larger; this difference does not exist in the deciduous dentition, in which the canines are relatively small.

The upper premolars are implanted by three distinct roots, as are also the true molars; the latter are quadricuspid, but lack the oblique ridge. The first lower premolar, by its front surface, articulates with the upper canine, and is of curious form. It is implanted by two roots, but the anterior root is produced forwards, so that the antero-posterior extent of the tooth is much increased. The apex of the cusp of the tooth is almost over the posterior root, and from this point the crown of the tooth slopes obliquely forwards down to its anterior root. This peculiarity in the form of the first lower premolar is eminently characteristic of the baboons. There is nothing to note of the second premolar save that it is implanted by two roots, like the true molars, which are quadricuspid; of them the third is larger than the first two, and is quinquecuspid.

But in some genera, *e.g.*, *Cercopithecus*, this is reduced in size and is tricuspid.

The anthropoid apes include the gibbons (*Hylobates*), the orang (*Simia*), the gorilla (*Gorilla*), and the chimpanzee (*Anthropopithecus*, formerly called *Troglodytes*); all of them have the oblique ridge upon the upper molars.

Upon the whole the gibbons are the lowest, and the gorilla or the chimpanzee the highest, of the anthropoid apes,* which are all confined to tropical areas. Thus the gorilla and chimpanzee are confined to tropical Africa, and the orang is limited to a part of the Malay archipelago. The gibbons are more widely distributed over the Malay archipelago and tropical Asia. Their teeth are not unlike those of man, except that their longer, slender canines extend far above the level of the other teeth.

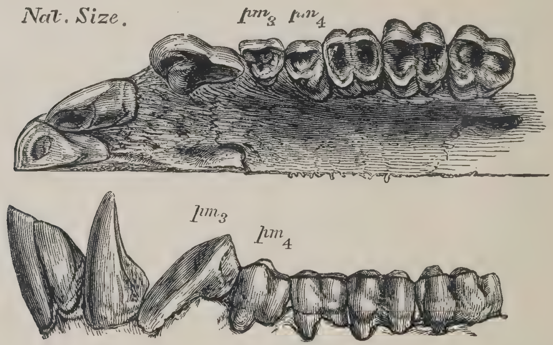

FIG. 309.—Upper and lower teeth of a monkey (*Macacus nemestrinus*, male). The length and sharpness of the canines, and the peculiar form of the anterior lower premolar, contrast with the aspect of the corresponding teeth in the anthropoid apes or in man.

Although the **Gorilla** on the whole approaches most nearly * to man, this can hardly be said to be the case with its dentition. The jaws are very square, and there is a large diastema in front of the upper canine, which in the male gorilla is of great size and strength, its tip descending far below the level of the alveolar border of the lower jaw when the mouth is shut.

In the lower jaw there is no diastema, but the teeth are all in contact with one another; the first of the premolars is a very strong pointed cone, showing plainly the close relationship between canines and premolars alluded to on a previous page.

The molars increase in size from before backwards, the third molars attaining to a very large size, and in the lower jaw all three have five cusps.

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* These statements are open to doubt.—H. W. M. T.

Nevertheless, though the teeth are coarser and stronger, there is a general resemblance to those of man.

It has been pointed out by the late Professor Rolleston that the canine tooth of the male anthropoid apes is a little later in coming into place than in the female. Thus in the male chimpanzee and orang it is not cut until after the third molars (wisdom teeth) are in place, whereas in the female it follows the second, but precedes the third, molars. The sexual difference in the canine teeth is very well marked in all the anthropoid apes, and its later eruption in the males is explicable both upon the ground that, being a sexual weapon, it is not needed prior to the attainment of sexual maturity, and also that, being of very large size, its formation might be expected to take a longer time. No such difference pertains to the milk dentition, in which the order of eruption is exactly that which is met with in man.

Sir W. Flower stated in general terms that the canines are the last teeth to be cut, but mentions that in the gibbons they come up at the same time with, or even precede, the third molar, and that this is also sometimes the case in the orang.

Dr. Magitot (10) combats the idea that there is any difference in the order of the eruption of the permanent teeth between man and the anthropoid apes, but, while his observations have been both careful and widely extended, he lays much stress upon an observation made upon a *female* gorilla skull, in which, as has just been mentioned, the order of succession is not quite the same as in the male.

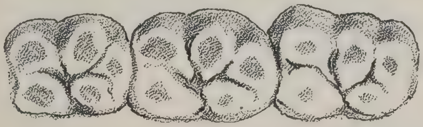

FIG. 310.—Slightly worn lower molars of a gorilla, showing the arrangement of the five cusps.

In a specimen of a New World monkey (*Cebus hypoleucus*) the author found m_3 on the point of erupting, whilst the temporary milk molars had not yet been shed, and the canine was not yet erupted.

Giglioli says that in a chimpanzee the order is the same as in man, but that in a male gorilla he found the canines and third molar erupting simultaneously, the former teeth, however, taking the longest time to fully erupt.

The dentition of the Orang approaches tolerably closely to that of man, and the points of resemblance and of difference may be fairly well seen in the accompanying figure (Fig. 311).

The first upper incisors are similar to those of man, but are larger; the second are, relatively to the first, much smaller, and are caniniform in shape, both inner and outer angles of their cutting edge being sloped off to such an extent that a central pointed cusp remains in place of a thin cutting edge. The canines are strong, pointed teeth, the cingulum and the ridge joining it with the apex of the cusp being well marked upon their inner sides. In the female the upper canine is about half as long again as any of the other teeth ; in the male it is yet longer.

The first premolar is a little more caniniform than that of man ; its outer cusp is long and pointed, and a ridge unites it with the anterior part of the inner cusp, which is feebly pronounced ; the second is a blunter and broader tooth. The premolars are implanted by three roots. The molars are not unlike the human teeth in pattern.

In the lower jaw the incisors are large and stout, the canines sharply pointed, with a well-marked cingulum, and a well-marked median ridge on the inner side of the crown. The first premolar is a shorter, stouter, and blunter copy of the canine, and can hardly be said to have an inner cusp. In the second premolar the inner cusp is as high as the outer, and the cingulum is elevated both before and behind till it almost forms two additional cusps, but both teeth have two distinct roots, which lie anteriorly and posteriorly like those of the lower molars. Indeed, there is no other dentition which exemplifies the transition from incisors to canines, from canines to premolars, and from premolars to true molars better than that of the orang.

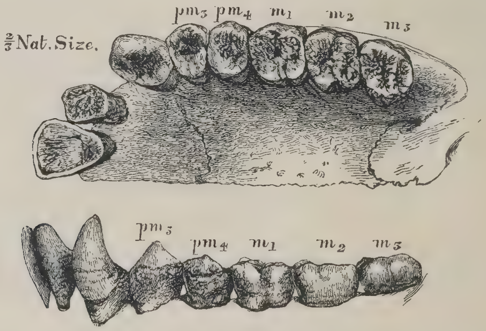

FIG. 311.—Upper and lower teeth of an anthropoid ape (*Simia satyrus* or *Orang outan*).

There is also a point of interest about the lower premolars which may be noticed here. If the lower first premolar of one of the anthropoid apes be examined, it will be found that its posterior root occupies the whole width of the alveolar border, but the anterior root when looked at from above is found to be of much less width, and does not extend inwards to much more than half the distance reached by the posterior root.

There is a form of abnormal root which is met with in the first lower premolar of man of sufficient frequency of occurrence to obviously have some significance. It consists in the outer border of the root towards its apex being folded forwards and inwards, so as to present an approximation to a double root at the end. The author has collected eighteen examples of this, and in two it has gone to the extent of a second small anterior root being completely formed.

Thus there is as a comparatively common abnormality a tendency to the formation of two roots, one anterior and the other posterior, and in every single instance it is the posterior root which is fully developed, and the anterior root is tending to be formed as a smaller root, on the outside quite level with the other, but not extending inwards in the direction of its width to nearly the same extent as the posterior root. In fact, it is trying to parallel the state of things which is constant in most anthropoid apes, and is hardly explicable on any other hypothesis than that it is a reversion, for in a reduced dentition like that of a xanthocroic man it is not conceivable that there should be a tendency to the development of a second root to the first premolar as a commencement of a new order of things.

The lower molars resemble those of man, save that their surface is marked by that finely wrinkled pattern which is common to all the unworn teeth of the orang. One is struck by the great backward elongation of the jaws, by their squareness, by the parallelism of the two sides, which converge slightly at the back, and by the large size of the teeth in proportion to the bulk of the whole animal.

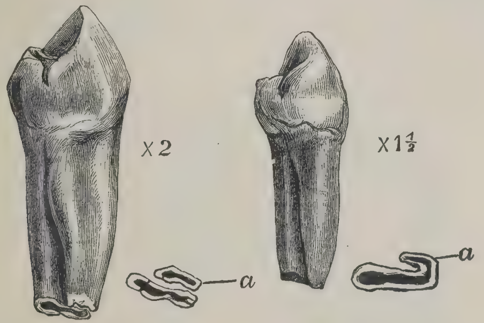

Fig. 312.—Left lower premolars (human). In the right-hand figure a second (anterior) root is in process of formation by a folding round of the flattened end of the root; in the left-hand figure it has attained to being a distinct root. *a*. Transverse sections of root.

The large size of the canines being in a measure a sexual character, is, as is so often the case, not very noticeable in the young animal; the accompanying illustrations of a young and an adult male orang may serve to show this, as well as some other differences developed by age.

Another peculiarity of the orang lies in the enormous length of the roots of its teeth; this is not shared by the gorilla, the roots of whose teeth are proportionately shorter, and the chimpanzee has roots far shorter and feebler than either.

Looking at the palatine surface of the jaws of an orang, the front of the mouth is somewhat square, and the premolars and molars stand nearly in a straight line, not, however, strictly parallel with those of the opposite side, as they approximate at the back, the third molars being nearer together than the premolars. In the gorilla the two sides of the "arch" are parallel, and in the chimpanzee they are also nearly parallel, with a slight approximation at the back.

So far as teeth go, the chimpanzee most nearly resembles man; the canines are not so large, and there is no very great sexual difference in the canines, and none in the general size of the whole animal.

Fig. 313.

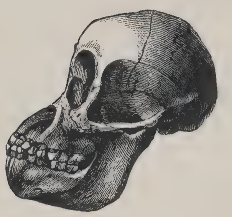

Fig. 314.

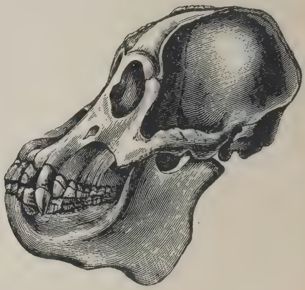

Fig. 315.

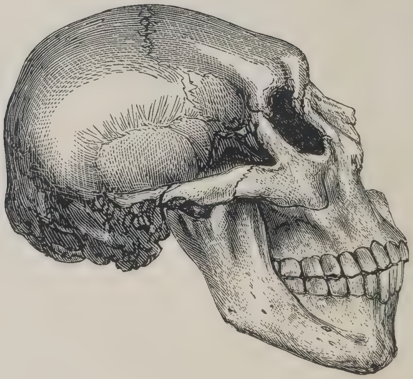

Fig. 313.—Skull of a young male orang. The upper canine does not nearly reach to the lower alveolar border.

Fig. 314.—Skull of adult male orang, in which the canine is largely developed.

Fig. 315.—Side view of skull of an idiot.

The teeth of the chimpanzee are not very powerfully developed, and the third molars are a good deal smaller than the other teeth; the lower premolars also have their two roots more or less fused.

The upper premolars are shorter in antero-posterior extent than those of other anthropoids, their outer predominate over their inner cusps, and in their position relatively to the molars they more closely follow the human type.

Another difference between the chimpanzee and the orang and gorilla lies in the comparatively early closure of the intermaxillary suture. This suture closes in man about the time of birth, in the chimpanzee about the time of the change of the teeth, whilst in the orang and gorilla it remains permanently open. Hence there is a greater capacity for forward elongation or increased prognathism in the latter and in the chimpanzee than in man, and this is related to the great size of the canines and the formation of the diastema which hardly existed in the temporary dentition.

There would appear to be a great deal of variability about the occlusion of the upper and lower teeth in the higher apes.

Thus in the Natural History Museum there are three orangs which are distinctly underhung, and several whose incisors present an "edge to edge" bite. There are also three underhung chimpanzees, as well as one which is underhung in the milk dentition, a thing exceedingly rare in man. There is also an underhung gorilla; and in the museum of the Royal College of Surgeons there is a gorilla's skull in which the lower jaw contains two supernumerary teeth buried in the substance of the ascending ramus, with their crowns looking upwards, close to the foramen where the inferior dental nerve and vessels enter the bone (11).

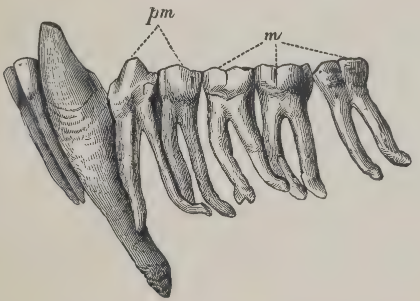

Fig. 316.—Lower teeth of *Orang*. From a jaw from which the bone had been removed, exposing the roots of the teeth.

There is a good deal of variability in the number of teeth in anthropoid apes, no less than 8 per cent. of the skulls examined by Bateson (1) having supernumerary teeth; in *Cebidæ* and *Ateles* he found them in 4 per cent., and in other New World monkeys he found none at all.

Rudimentary supernumerary teeth are not uncommon in the gorilla. From their position Duckworth (5) suggests that they may represent the extra premolar of the Platyrrhine monkeys.

The differences which serve to distinguish the dentition of the most anthropomorphous apes from that of man are mainly these. Relatively to the size of the cranium, and of the whole creature, the teeth and jaws are very much larger in all their dimensions; hence the creatures are prognathous, and the facial angle small even as compared with the jaws and cranium of an idiot. As might be expected, this difference is not so great in the young as in the adult animal.

In place of the teeth being arranged in a sweeping curve, the jaws are more square in shape, the incisors being arranged in something approaching to a straight line between the two great outstanding canines, behind which the premolar and molar series run in straight lines, converging somewhat as they pass backward. There is a "diastema" * or interval in front of the upper canine, into which the point of the lower canine passes, when the mouth is closed. Both the greater squareness of the jaws and the existence of the diastema are direct results of the great size of the canines, and are consequently not marked in young specimens.

The upper premolars are implanted by three roots, the lower by two roots, just like the true molars, and the premolars, when unworn, partake more of the pointed character than they do in man.

The third molars present the same pattern of cusp surface, but are larger than the other molars in the gorilla and the orang, and there is abundant space for them, so that they play an important part in mastication. The molar teeth of these apes are also more square, their cusps sharper and longer, and the characteristic patterns more strongly pronounced, than in man. Moreover, the intermaxillary bone is more largely developed, and the intermaxillary suture remains distinct through life, except in the chimpanzee.

Anthropidæ.—In passing from the apes to the lowest of mankind, there is a somewhat sudden change in the character of the dentition ; but while it cannot but be admitted that there is a gap, the differences are rather of degree than of kind.

As the canine is less largely developed, there is no diastema nor any sexual difference in dentition, no tooth projecting beyond its fellows, so that the teeth are arranged in an unbroken arch. The premaxillary bones become fused with the superior maxillary soon after birth, whereas in the chimpanzee they become fused on the completion of the second dentition, and in the gorilla and orang they remain distinct.

It is generally said that in man the molars decrease in size from before backwards ; that is to say that the first molar is the largest, while in anthropoid apes, with the exception of the chimpanzee, the contrary is the case. Though this is on the whole true, it requires some qualification ; thus in certain lower races, such as the Australian blacks, the second and third molars are not smaller than the first, and in the palæolithic man of Spy they are actually larger. The molars increase in size as they go backwards instead of diminishing, and their three roots are very distinct characters which are simian and are only shared by a few low races (*e.g.*, Australians), in which the last tooth is as big as the others. The transverse diameter of the molar is contracted in its posterior half, a simian character, and the canines are very large. On the whole we may say that in the Neanderthal man we have a greater number of simian characters than exist together in any living man, though each of the characters may be met singly in other low types of mankind.

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* Something approaching to a diastema is said to have been observed by Vogt and Broca in early European skulls.

Palæolithic man was also characterised by a want of chin, so that, seen in profile, the lower jaw at the symphysis slopes backwards, and resembles that of an anthropoid ape.

One of the features by which the lower races of mankind differ from the higher, and resemble so far the anthropoid apes, is the prominence of the lower part of the face, in fact, the large development of face as compared with cranium. The degree of prognathism, as this is termed, may in a rough way be described as being the amount by which, the skull having been placed in its normal position, the lower part of the face projects beyond a vertical line dropped from the forehead.

But such a rough method would be obviously unsuitable for comparison and measurements, so Camper many years ago devised a method of measuring what was termed the "facial angle." He drew a line through the external auditory foramen along the floor of the nose, producing it beyond the nares. A second line was drawn from the forehead between the supraorbital ridges down to the edges of the incisor teeth, this line crossing the first near where it emerged from the nares; the angle included between these lines at their intersection was called the facial angle. This gave an angle of about 20° for a dog, 85° for an Australian black, 95° for a European, and the Greeks used an angle of 100° or more to express their ideal of beauty and of intellectual power.

Camper's facial angle gave a general degree of prognathism which might sometimes be largely due merely to the inclination of the teeth, or be influenced, as in the gorilla, by the size of the supraorbital ridges; and almost every conceivable variety of points of measurement has been used by one or other observer, so that "facial angle" gives no precise information unless the points of measurement are specified.

Jacquart took Camper's horizontal line, but drew his vertical line from the forehead to the centre of the lower edge of the alveolar border, thus eliminating the influence of the teeth themselves, but comparative measurements taken on these lines gave such small differences of angle that they did not seem worth the trouble of taking and recording. Others drew their horizontal line from the point between the occipital condyles along the floor of the nose, others again from the auditory foramen obliquely down to the points of the teeth, &c.

The discrepancies due to the almost infinite variety, within small limits of the points chosen, led to anthropologists somewhat unduly neglecting the facial angle, and it is now generally differently expressed.

A line may be drawn from the middle of the front margin of the occipital foramen (*basion* of Broca) to the root of the nose (*nasion* of Broca), and measured. This of course can be done on an intact skull by means of well-bowed callipers, and is called the *basionasal length*. A second measurement is taken from the same point (*basion*) to the middle of the front edge of the alveolus; this is called the *basi-alveolar length.*

The former being taken as 100, the so-called *alveolar*, or *gnathic, index* is got by multiplying the basi-alveolar length by 100, and dividing by the basionasal length:

$$\frac{\text{Basi-alveolar length} \times 100}{\text{Basionasal length}} = \text{Gnathic Index},$$

and the results thus set down :—

Orthognathous when it is below 98.
Mesognathous when it is 98·1 to 103.
Prognathous when it is above 103.

This method, due to Sir William Flower, seems the most satisfactory and is largely adopted, but unfortunately there is still a want of unanimity amongst anthropologists, and other measurements are still met with for which the reader must be referred to manuals of anthropology.

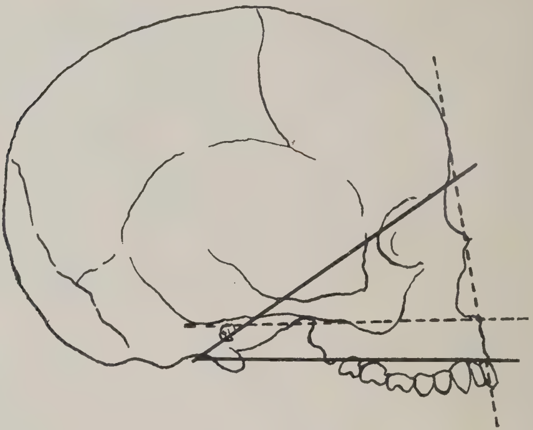

FIG. 317.—Diagram of two of the methods of estimating the facial angle. The dotted lines represent those suggested by Camper, the full lines those along which measurements for ascertaining the gnathic index are taken.

Although it is true that the lower races of mankind are more often prognathous than the higher, yet it is not universal with them. The few palæolithic skulls which have been found are prognathous, but the Veddahs of Ceylon (a very low race), the Andaman Islanders, and the Bushmen, are all orthognathous, so that it would appear that orthognathism had been attained by some otherwise low races and afterwards lost again or else that these races are not upon the same direct line of descent as the somewhat higher races who are prognathous.

In some of the palæolithic men the prognathism, otherwise considerable, is, just as in the gorilla, diminished by the huge supraciliary ridges, and although the alveolar borders are prominent and the lower jaw massive, yet there is a falling away below this, as the chin was very feeble.

It seems possible that prognathism is related to the period of closure of the intermaxillary suture, for in the gorilla the antero-posterior length of the premaxilla increases from 19 mm. at the period of complete deciduous dentition to 22 mm. in the female and to 27 mm. in the male at the period of adult dentition, in the orang from 11 mm. to 15 mm. and 18 mm., and in the chimpanzee from 8 mm. to 14 mm. and 19 mm., whereas in man no growth takes place in this region (11). No material is available for ascertaining whether the intermaxillary suture is late in closing in the prognathous lower races of mankind, but it is noteworthy that persistence of the suture, though rare, is sometimes met with in them.

Almost the whole forward elongation is accounted for in the chimpanzee by the growth of the premaxilla, but this is not so in the orang and gorilla, in which there is also growth of the edge of the maxilla. This elongation of the premaxilla and maxilla obviously has relation to the extent of the development of the canines and of the formation of the diastema, being much greater in the males than in the females.

Hence in this respect, as in others, the deciduous dentition of anthropoid apes more closely resembles that of man than do their respective permanent dentitions, and the chimpanzee, with its short premaxilla, at the earlier period most resembles man.

Of living races of mankind, it may almost be said that if we wish to find an absolutely typical human dentition, we should go to the lower races, as in the higher a process of reduction seems to be taking place.

Although of late years the additions to our knowledge of early man have been neither few nor inconsiderable, the material available is still fragmentary and incomplete, and the time has not yet arrived when it is possible to draw up a comprehensive statement of the characters of his dentition, and, still less, to trace out the evolutionary stages by which it has been reached. With regard to this latter aspect of the question difficulties arise from the uncertainty of the comparative dates of various specimens and also from the paucity of the remains of the higher apes, amongst which it seems probable that none which are known to us at the present are the actual precursors of the human race. But from analogy it would seem to be a reasonable expectation that the teeth of the earliest men would be fairly uniform in character, and that they would resemble in the main the well-developed and supposedly typical human teeth found in the lowest existing or recently extinct races, such as, for instance, the Tasmanian blacks. In correspondence with a yet ruder manner of life, they might be expected to be more powerful and to present a closer resemblance to the teeth of the anthropoids. In such a dentition the incisors, especially the upper incisors, would be large and wide and would meet the lower incisors in an edge-to-edge bite; the canines would be large and long, the upper molars all provided with four and the lower molars with five cusps, whilst the third molars would not depart from this typical pattern and would be of a size at least equal to or greater than the first and second molars. But these expectations, reasonable though they might appear, are only partially fulfilled by the specimens of very early man as yet known, so that the facts do not admit of being cast into any such simple statement. Examples of reduction in the cusp formula occur amongst some otherwise quite powerful dentitions, and there are many other variations the origin and outcome of which we cannot trace.

It is quite certain that man existed in very early Pleistocene times and before, at all events, the later glacial epochs; it is certain also that he was then fully man, so that his ancestral forms might be looked for at a still earlier geological period. But no remains have been found which can with any certainty be referred to the Pliocene period, although some have a doubtful claim to that degree of antiquity.

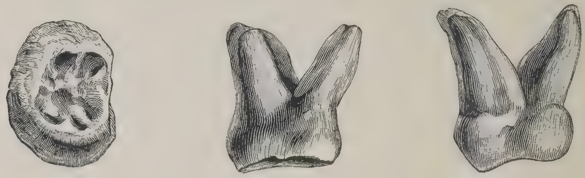

FIG. 318.—Upper molars of *Pithecanthropus* (natural size). The masticating surface of the third molar is on the left, while the front view of the same tooth is on the right. The other molar with a worn surface is in the middle (front view). Drawn from casts made by Mr. Booth Pearsall.

Pithecanthropus erectus.—In 1891 Dr. Dubois discovered in Java a portion of a cranium, a femur and two teeth, and a third tooth was subsequently found in the same locality. These remains nowadays are accepted as human, although at first some controversy raged over them, certain naturalists considering them to be the remains of an ape; to these remains Dubois gave the name of *Pithecanthropus*, or Apeman. He considered them to be of Pliocene age, though a later expedition referred them to early Pleistocene; but it is difficult to compare with exactitude the ages of strata in a tropical country with those in a temperate zone. The teeth have been considered to be the teeth of the orang, and a human second upper molar and a third molar, or two third molars of opposite sides. A study of excellent casts given to the author by Mr. Booth Pearsall convinces him that he is right in considering them to be both third molars: one is worn into a concave depression, the other is unworn, but this does not necessarily imply that they did not come from the same mouth. One may have been erupted a little later than the other, or this may have happened to its opposing lower tooth, or there may have been some imperfection in the articulation of the teeth with one another. The bulbous prominence at the back of each tooth and the absence of any facetting of this surface are clear indications that no tooth stood behind either of them. In both of them the masticating surface is smaller than the rest of the crown, the neck is well defined, the roots are thick and stout, but not of unusual length, whilst the outer pair of roots (labial) show more or less fusion. The two outer roots of the worn tooth show on a cross section of a cast a decided tendency to division into three, which is unusual. The inner or lingual roots of both of the teeth are thick and flattened.

The teeth are not exactly like any known teeth, either human or simian, and it may be added that most writers have considered the worn tooth to be a second upper molar rather than a third molar. So far as the size of the cranium can be estimated from the portion preserved, the teeth were rather large as compared with it. Their dimensions are as follows : the worn tooth at its widest part measures in antero-posterior diameter 12 mm., and in transverse diameter 14 mm., and its total length is 20 mm., of which the roots make up about 12 mm. The unworn tooth has an antero-posterior diameter of 12 mm. and a transverse diameter of 16 mm. Its total vertical length is 21·5 mm., of which the roots make up 14 mm.

No definite cusp formula can be assigned to them, so that they fail to comply with the expected conditions, and appear in this respect to have undergone reduction.

Eoanthropus Dawsoni.—This name has been given by Dr. Smith Woodward to remains found in a river gravel of high antiquity and in association with a Pliocene elephant's molar, a water-worn mastodon tooth, fragments of two hippopotamus teeth, and a molar of a Pleistocene beaver. The age of the deposit cannot as yet be determined with certainty, nor is it certain that the gravel was the original location of the remains. There is a doubt whether it is justifiable to create a new genus for this man, the restoration of the missing parts under Dr. Smith Woodward's directions representing a greater departure from the ordinary human type than those carried out by Professor Sir Arthur Keith. Hence if the latter be the more correct the name should be rather *Homo piltdownensis.*

The remains found consist of nearly half of the mandible and considerable portions of the cranium, most of the face, however, being wanting. The mandible contains the first and second molars of the right side and the empty socket of the third ; in front of the first molar the alveolar portion of the jaw is broken away, but the lower border is complete as far as the symphysis, and shows, in its forward slope, an absence of chin more complete than in any other human jaw that has been found. In fact, the contour of the front of the mandible is exactly that of a young chimpanzee. The teeth, however, are quite human, both having five well-defined cusps and two normal well-separated roots. The crowns measure respectively in the antero-posterior direction 12·5 mm. and transversely 11 mm.* : the groove marking the anterior and posterior cusps is well marked and is carried down on the outside of the teeth, the grooves mapping out the fifth cusps being also distinct. The third molar had two distinct roots, of which the posterior is the smaller, but these roots might have carried a crown as large as the first and the second molars.

The coronoid process is large and indicates the presence of a very powerful masseter muscle, but though the tops of the teeth are worn flat, showing that the jaw was capable of free side-to-side movement, the wear is not excessive, and barely exposes the dentine, notwithstanding that the third molar was fully erupted. From this, and from the fact that the first molar is not much more worn than is the second, it may be inferred that the diet was not of a gritty nature. It has been conjectured that, judging from the form of the mandible, the teeth in front of the molars must have been large ; in other words, that it would have taken large teeth and perhaps a very large canine to fill the space. But here there is a difference of opinion, and as an upstanding canine limits lateral movement, the flatness of the molars indicates that it could not have risen much above the general level.

The molars being long in proportion to their width "must be regarded as reminiscent of the apes in their narrowness." They also in this respect resemble the isolated tooth found at Taubach, which has been regarded by some as perhaps the tooth of a pithecoid ancestor rather than of fully evolved man, though numerous palæolithic implements have been found near to it.

Professor Sir Arthur Keith's restoration gives not only a much larger cranial capacity, but also a less ape-like mandible, though unquestionably the form of the latter does approach the anthropoid form more closely than any other human mandible yet discovered.

At a later date a canine tooth was found and described by Dr. Smith Woodward at the British Association Meeting, 1913. This is said, whilst not of a length to project above the general level of the teeth, to present in its manner of wear and in its shape marked simian characters. With regard to the controversy as to the restoration of the entire skull and its resultant cranial capacity, Dr. Smith Woodward, whilst admitting that a mistake was originally made in locating the middle line, maintains his contention that the cranial capacity was small, and not, as according to Sir A. Keith's restoration, large. For he holds that other alterations, more or less directly arising out of the alteration of the middle line, compensate the increased dimensions at that region by the diminution of other dimensions. So the controversy as to the extent to which *Eoanthropus* approached the apes is still unsettled.

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* The measurements given in the text were taken by the author, and represent the points of maximum size of the crowns. Smith Woodward gives smaller measurements, viz., for the first molar, 11·5 mm. length, and 9·5 mm. width ; and for the second, 12 mm. length, and 10 mm. width. Probably the discrepancy arises from his having measured the dimensions of the flattened worn surfaces and not the greatest convexity of the teeth.

[The **Talgai Skull** described by Dr. S. A. Smith (12) was found in the Darling downs of South Queensland, and is probably of Pleistocene age. The cranial and facial skeleton are of the Australian type, while the palate and teeth present "certain characters more ape-like than have been observed in any living or extinct race except that of *Eoanthropus*." The teeth present in the Talgai skull are two canines, two left premolars and a first and second molar of both sides; two wisdom teeth are unerupted, but have been exposed. The mandible is missing. The premaxillary region is extremely broad and square, and protrudes forwards and downwards in direct continuation from the nasal floor. The large incisors are in almost a straight transverse line, the canines stand out prominently at the corners, and the series of cheek teeth are almost parallel on the two sides. This quadrangular shape of palate is more marked than in any present day Australian types and is strongly reminiscent of the anthropoid condition.

The upper incisors, though extremely large, are within the range of variation of the present day examples. There is obviously no diastema. The canine is in some respects the largest single human canine yet recorded. It is distinctly human in shape, though its premolar facets differ from those of other known human teeth, but are comparable with the facets found on the canine of the young orangs.

The length of the premolar series is greatly in excess of the average for living races. The teeth are typically human and extraordinarily large. The molar crowns also are of great size, and approach in size the largest of the Krapina specimens. The roots are separated up to the necks, and the pulp cavities are small. The first and second upper molars are of almost equal size. The wisdom tooth is large, but with the usual characteristics of an unerupted tooth.

"The size of the Talgai palate, especially of its anterior portion, and the size and relations of the canine teeth are features which are quite outside the range of variation observed in any other human skull, except that of Piltdown."]

Homo neanderthalensis.—As long ago as 1857 the famous Neanderthal skull was discovered, and from that time forward the existence of a well-marked type of a low grade has been recognised, and the Neanderthal race has been freely spoken of. With its cranial and other characters we are not here concerned; suffice it to say that the supraorbital ridges were very strongly pronounced and the forehead so retreating that it is not very conspicuous from the front. This with the retreating chin must have given a snouty aspect to the face; there were also peculiarities in the long bones. Since that time a good many of the skulls found have been unhesitatingly referred to the Neanderthal race, but the uniformity in the teeth which might have been expected amongst those having similar cranial and facial characters does not exist. On the contrary, considerable difference is found in the teeth. For many years it has been held that the Neanderthal race were the ancestors of modern man, but recently doubt has been thrown upon this.

In 1907 Dr. Gorganovič-Kramberger discovered in a cave in Croatia, near the village of Krapina, a number of remains, amongst them being no less than 230 teeth; the remains are referred to the Neanderthal type. The crowns of the teeth do not differ much from those seen in recent Negroid races, but their roots are large, and in about 50 per cent. the multiple roots show a strong tendency to be fused into a single mass. It would be possible to match these teeth with fused roots from a collection of abnormal recent teeth, but here it occurs sporadically, whereas in the Krapina teeth the whole set is affected, and even the single-rooted teeth show an overgrowth of root. The Krapina molar teeth have no constriction at the neck, and have very large pulp cavities.

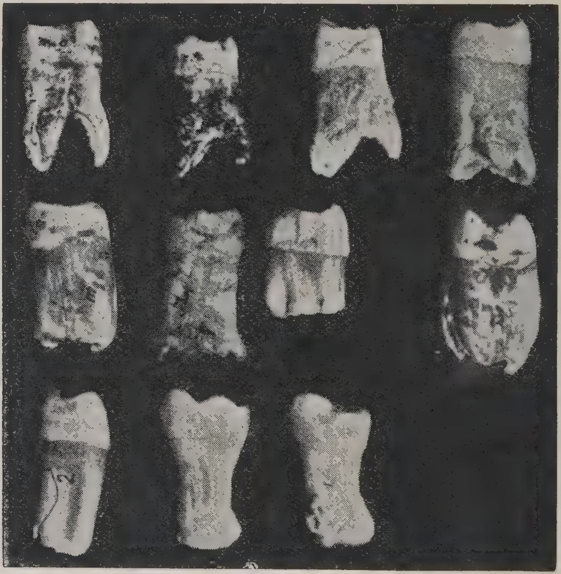

Fig. 319.—Some molar teeth of Krapina man. The upper two rows are upper; the lower row, lower molars. (After Bryce, Brit. Dental Journ., 1913, p. 107, after Gorganovič-Kramberger, Anat. Anzeiger, Bd. xxxii.)

More recently a fairly complete set of teeth have been found in a cave at St. Brelade's in Jersey, which have been very carefully described by Keith and Knowles (8), and these present the same overgrowth of roots. Hence the Krapina teeth must be admitted to be a real type and not a freak. But so peculiar are these teeth that Adloff maintains that they would never have got back to a normal type, and hence that the Krapina race cannot lie on the line of descent of modern man, but Kramberger does not agree with this inference. It must be remembered that only 50 per cent. are markedly so affected, and the skiagraph published of a jaw with the teeth *in situ* shows that in this specimen the teeth had roots neither fused nor abnormally large. The lower molars are not in a marked degree five-cusped, and the third molar is smaller than the first and second molars.

Passing to the consideration of the Jersey teeth, the configuration of their crowns and the facets of wear at the points where the contiguous teeth touch one another seem to indicate that the upper jaw and palate must have been wide and of somewhat horseshoe form. This is often found in, and was perhaps a characteristic of, the Neanderthaloid jaw. The Jersey teeth resembled those of Krapina in the absence of a constricted neck, the necks in some cases actually exceeding the dimensions of the crown, and some of the roots are just as thick. Another feature was the early contraction of the pulp cavities by secondary dentine, even at a time when the cusps are only slightly worn down.

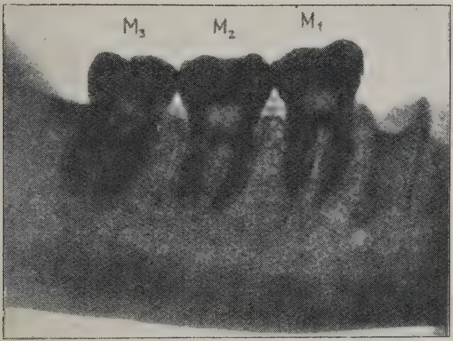

Fig. 320.—Skiagram of Krapina teeth. (After Gorganovič-Kramberger, Anat. Anzeiger, Bd. xxxi., after Bryce, Brit. Dental Journ., 1913, p. 107.)

The lower canine is a remarkable tooth : the roots are very large indeed, and furrowed, indicating a tendency to division into an outer and inner root. The first lower premolar is a larger tooth than the second and has a larger root with a tendency to division, thereby recalling the dentitions of the anthropoids, in which the first premolar, occluding partly with the upper canine, is larger than the second, and is highly specialised ; in modern races this relation of size is reversed. In general there is a fairly close correspondence in size of the teeth of this *Homo breladensis* with those of the Heidelberg jaw to be presently alluded to.

In some of the incisor and canine teeth the cingulum at the inner surface is well developed (cf. p. 523), and on the canine it forms a definite lingual cusp, so that the transition from the incisor form to the premolar form of crown is evident. This is notably the case in the skull described by Klaatsch (9) found at Dordogne, in France, and in the canine and first premolar of the Heidelberg jaw, in which a vertical ridge down the back of the canine is conspicuous. A similar condition prevails in many of the Krapina teeth.

In the development of a normal tooth the pulp, after the crown has been formed in the case of a single-rooted tooth, is reproduced on a gradually diminishing scale, so as to form a tapering root, or in the case of teeth with multiple roots in areas corresponding to the several roots. In these teeth with big roots the pulp goes on growing down without the usual reduction in size, or, in teeth with multiple roots fused into a block, it fails to grow out on the separate lines corresponding to the roots, but remains of full size and without the constriction which marks the neck.

In the opinion of Professor Sir Arthur Keith these teeth with massive roots are an adaptation to meet excessively hard use, such as is indicated by the massive masseter muscles; no doubt, in the case of the single-rooted teeth, the extra bulk of the root would give greater firmness of implantation, but it is open to question whether a tooth with normally multiple roots would gain by their fusion into a block. For it is clear that the division of the roots and their divergence distribute the pressure to which the tooth is subjected and resist movement in various directions. The single block imbedded in an exceptionally thick alveolus would seem to be a clumsy way of attaining firmness of implantation and ill adapted to wide excursions of the mandible in chewing.

Homo heidelbergensis.—The Heidelberg mandible was found in the Mauer sands of early Pleistocene age. It is an exceedingly massive jaw with an immense coronoid process, so that the masseter must have been of great size, twice as big as in modern man. The chin receded, so that it may be said to have no chin, though the backward slope is not so extreme as in the Piltdown skull. The teeth are large, though not so very much larger than in some modern low races, and the canine did not stand up above the level of the other teeth. The teeth are somewhat peculiar in form, the necks being nearly as large as the crowns and the roots massive, and showing a tendency to fusion in those with normally multiple roots. The first molar is 12·5 mm. in antero-posterior and 10·3 in transverse measurement, but the fifth cusp is not very distinct either on this or on the other two molars; all the teeth are considered however to possess five cusps, and the three are about the same size. On one side some of the molars have been broken by their strong adhesion to a pebble, and the fractured teeth show that the pulp cavity was large and not at all encroached upon by secondary dentine. A skiagram of the teeth shows that the roots of the first two molars were perfectly distinct, though it also shows that the pulp cavities were large and continued downwards of fairly large dimensions. However, in this respect the Heidelberg teeth are far less peculiar than the Krapina or the St. Brelade's teeth, so no more need be said on that head.

The canine and first premolar present gradated characters, both having a well-marked cingulum and a distinct median ridge running down their lingual surfaces.

Large though the teeth are, they are by no means crowded in the jaw; it has been said that there is room in the jaw for even larger teeth. The incisors and canines are more worn down than the premolars and molars, so that the teeth may probably have been largely used for gnawing.

At Spy, in Belgium, there were two skulls found, both referable to the Neanderthal type, but showing some advance upon the Heidelberg jaw. The teeth are smaller, have a more defined constriction at the neck, and the roots are not of excessive size, nor are they at all fused. There is still an absence of chin and a broad coronoid process, and the front teeth are inclined forwards. The teeth, however, are of more modern type, and are not conspicuously more powerful than those of modern man; and the three molars are almost identical in size. Kramberger gives their cusp formula as four cusps on each of the upper molars, five cusps on the first lower molar, and four on the second and third.

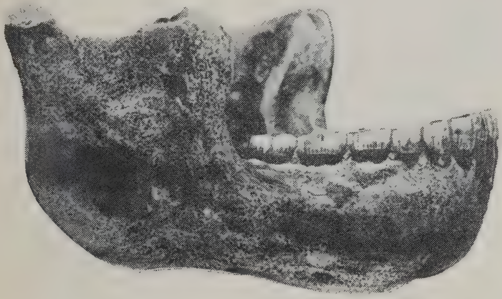

Fig. 321.—The Heidelberg jaw. (From Bryce, after Schœtensack.)

As of late years many inferences have been based upon the characters of Neanderthal teeth, which have been used as an argument that recent man cannot have descended from that race, but belongs to a separate stock which in early times supplanted Neanderthal man, who died out, it is necessary to discuss their nature more closely. Professor Sir A. Keith (⁷), whose opinion is worthy of the utmost respect, after entertaining the contrary view, has become a convert to this idea of supersession, and no longer regards Neanderthal man as upon the direct line of descent. But there remains a good deal to be said on the other side. In the first place, although some observers claim that in all Neanderthal teeth a peculiarly large and deeply extending pulp cavity can be traced, only 50 per cent. of the Krapina teeth on external examination presented peculiarities of the roots in any marked degree. And the skiagraph published in Kramberger's work shows teeth with roots quite distinct, and not abnormally large. Hence even within the limits of the Krapina race there was a capability of wide variation from teeth of the massive type to others which would almost pass as of modern type. And whilst the peculiarity was common in the Krapina and the St. Brelade's remains, and affected large numbers, perhaps all, of the teeth of an individual, it can be found occurring sporadically in modern teeth, some of which can be found to match the Krapina teeth. Without going so far as to contend that the occurrence of massive teeth in modern man is a reversion, this capability of variation both in modern and ancient dentitions might be used as an argument on the other side, namely, that there is no difficulty in supposing that Krapina teeth could attain the modern type, and therefore that they do not afford a strong argument against Neanderthal man being on the line of descent.

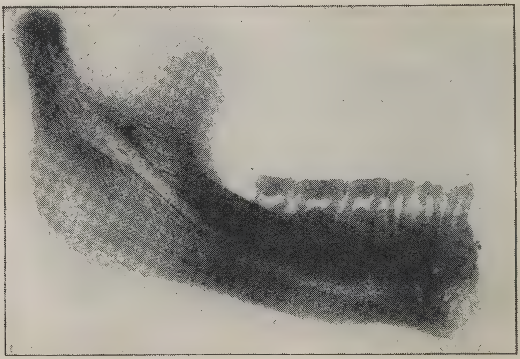

Fig. 322.—Skiagram of the Heidelberg jaw. (From Bryce, after Schœtensack.)

Again, Sir Arthur Keith, comparing skiagrams of modern teeth (the three lower molars) with the Heidelberg and the Krapina teeth, points out that even in recent man in passing from the first to the third molar the "pulp cavity tends to enlarge at the expense of the roots, and that the body of the tooth tends to become more and more imbedded within the alveolar process." But there is a possible source of fallacy: it must not be forgotten that the size of the pulp cavity decreases with age, and that the first molar in recent man is six years older than the second, and from twelve to fourteen years older than the third. Unless then the teeth examined belong to a much more than adult individual a progressive difference in the size of the pulp cavities is only to be expected. Moreover, the Krapina teeth used in this diagram are not even adult, the third molar not only not being erupted, but having only a portion of its crown yet formed; hence the difference in the size of the pulp cavities may be exaggerated. Still, whether the inferences drawn be correct or not, there is no doubt that many of the teeth of Neanderthal man do present characters which differ from those found in modern man.

It appears certain that during the persistence of the Neanderthal type, with its low retreating forehead, hardly visible from the front, its beetl'ng brows, its broad and snout-like face, with an absence of chin, the teeth underwent considerable modification, so that it is difficult to assign definite dental characters applicable to the entire race. As a working hypothesis it used to be generally assumed that the Neanderthal race are the ancestors of later and higher races, and, so far as it goes, the power of adaptive modification seen in their teeth lends support to the possibility of this idea. But there is some evidence that the Neanderthal race existed side by side with a people much more advanced, who may have supplanted them. The chain is very far from being complete: in the very ape-like Piltdown mandible we meet with teeth more like the modern human type than

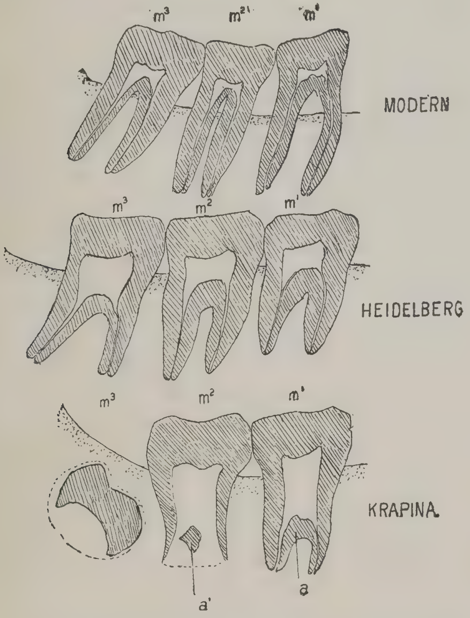

Fig. 323.—Drawings from skiagrams of the lower right molars of (1) modern European; (2) Heidelberg mandible; (3) Krapina mandible; *a*, *a'*, inner root system. 1 and 2 after Schœtensack; 3 after Kramberger. Natural size. (From Prof. Sir A. Keith's paper, Proc. Roy. Soc. Med., Odontolog. Sect., 1913, vol. vi., p. 105.)

we do in many other less ape-like Neanderthal jaws, and the very variable amount of wear displayed amongst the various specimens points to the foods consumed having been different.

Not only is the total degree of wear variable, but it fell with varying force upon different teeth ; thus in the Heidelberg mandible the incisors and canines are more worn than the premolars and molars, from which it may be inferred that the canine was cut some time before the third molar. It seems certain that Neanderthal man was a hunter and subsisted largely upon animal food, which would not entail severe wear of the teeth, except perhaps of the front teeth, which might be worn by the grinding of bones.

Professor Sir A. Keith attributes to an upstanding canine great importance as acting as a sort of steady pin and preventing lateral displacement of the lower jaw, though at the same time preventing much lateral movement in mastication. From the fact that the canines in primitive jaws like those of *Homo breladensis*, the Heidelberg jaw, and other Neanderthaloid jaws do not stand materially above the other teeth, he infers that side-to-side grinding motions of the jaws had already been fully acquired, whilst in recent races the overlapping of the upper incisors by the lower incisors passing behind them has again limited the freedom of side-to-side motion. In the older races there is a decided tendency to what is termed an edge-to-edge bite of the incisors, and this appears to have persisted even after the teeth themselves had attained to a modern type.

Of the relation in time between the eruption of the canine and of the third molar Professor Keith writes : "The extreme retrogression of the human canine teeth and their assumption of partial incisiform function and shape have led to the appearance of the permanent canine in him at an earlier (relative) date than in the anthropoid apes. The human milk canine, as in all Primates, cuts the gum with or even after the last milk molar, but the permanent canine cuts not last, as in Macrodont (*i.e.*, progressive as against retrogressive dental development—I count the gorilla and *Cynocephalus* as typical of Macrodonts) Primates like the male gorilla or orangs, but with or even before the second molars. In chimpanzees, especially in the females, the permanent canine cuts with or before the last molar. The date of its appearance depends on the period of preparation necessary for its development and growth, and there is no reason why it should not appear in man after the incisors and before the premolars, except that it is the descendant of an enormous fighting tooth which formerly was not required until the animal had reached its full fighting strength." These are the result of observations made upon about 150 anthropoids.

It is remarkable that in some ancient and powerful human dentitions an amount of cusp reduction, exceeding that seen in recent Negroid races, is already met with. But this is less surprising when we find that cusp reduction is to be found amongst the anthropoids, as is well exemplified in the following tables (hitherto unpublished).

which Professor Keith has most kindly placed at the disposal of the author. They embody the result of the examination of a large number of European, Negroid, and ape dentitions found in London and provincial museums, and in order to express the greater or less degree of cusp development he had adopted a decimal form of record :—

Upper Molars.	Normal Cusps = 4.		
	M_1	M_2	M_3
Negro	4	3·95	3·80
European . . .	4	3·75	3·60
Cynocephalus . . .	4	4	5
Gorilla	4·4	4·8	5·1
Orang	4	3·95	3·65
Chimpanzee . . .	4	3·92	3·55
Gibbon	4	3·9	3·75
Macacus . . .	4	4	4

Lower Molars.	Normal Cusps = 5.		
	M_1	M_2	M_3
Negro	4·9	4·5	4·9
European . . .	4·9	4·4	4·48
Cynocephalus . . .	5	5	6
Gorilla	5	5·2	5·3
Orang	5·07	5·1	5·5
Chimpanzee . . .	5·1	5·2	4·95
Gibbon	4·85	4·9	4·8
Macacus . . .	4	4	4·3

From these tables, abridged from those furnished to the author, it is seen that the gorilla and the dog-faced baboon (*Cynocephalus*) show some redundancy of cusps, whilst the orang and chimpanzee show some reduction. It also appears that the reduction, or the reverse, in cusps is not always similar in the upper and lower jaws. Thus *Macacus* has normal cusps in the upper jaw, but shows considerable reduction in the lower ; the orang and the chimpanzee show the reverse, namely, some reduction in the upper jaw and some redundance in the lower.

Whilst in comparing the gorilla and *Cynocephalus* with the orang and chimpanzee cusp reduction is associated with a less powerful dentition generally, it seems not to be quite a universal rule. In the Heidelberg jaw, in which the teeth are powerful, all three molars possess the five normal cusps, but there are others in which this is not the case.

[**Homo rhodesiensis.**—One of the most interesting discoveries of early human remains is that of a skull, a sacrum and portions of the leg bones which were found in a cave at the Broken Hill mine in North-west Rhodesia. These remains were found associated with rude stone and bone implements and with the bones of animals similar to those which still exist in that part of Africa. The skull is remarkable for the great size of its facial portion and of its massive and laterally extruded supraorbital ridges, the latter feature being more marked than in any other known human skull. The palate is well arched, and the upper teeth are placed in a regular horseshoe-shaped series. The lower jaw is missing. The central incisors are much worn down by an obviously edge-to-edge bite, and their pulp cavities are filled with secondary dentine. The left lateral alone is present and is much affected by caries, as are most of the premolars and molars; indeed, the third molar of the left side is the only one apparently quite unaffected. The third molars are distinctly smaller than the anterior teeth of the molar series, thus resembling the higher and differing from the lower races of man.

No detailed account of the individual teeth has yet been published, but from the wearing down of their occlusal surfaces and from the extent to which the teeth have been affected by caries it is scarcely possible that such can be anticipated.

Neither the geological age nor the systematic position of these remains has been definitely determined. The characters are to a large extent Neanderthaloid, but the brain case and the relative position of the foramen magnum are markedly different; hence they are regarded as belonging to a different human species.*]

Galley Hill man was found in an ancient river terrace containing palæolithic implements in abundance, associated with a mixed fauna comprising the lion, hippopotamus, woolly rhinoceros, and mammoth. Since the deposition of this terrace the Thames has worn its valley down 124 feet, so that this man is of great antiquity.

The remains generally, and the teeth in particular, are of nearly modern type so far as they are known. The first lower molar is only 11 mm. in antero-posterior dimensions and the second and third 10·2. In Keith's earlier work it is stated that the first molar has five cusps and the second and third only four, but in a more recent paper which embodies his later views they are all three said to have five cusps. The teeth being somewhat worn, there is room for uncertainty, and in his original diagram the fifth cusp on the third molar is marked with a query, but on the whole his later view may be accepted with the proviso that the fifth cusp is not very well marked, though the general contour of the crown seems to provide for its presence. Galley Hill man has always presented a difficulty. If we accept the evidence of its age it was more modern in type than was to be expected, for it is older than many Neanderthal specimens;

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* For a detailed account of these remains the reader is referred to the account given by Dr. A. Smith Woodward, F.R.I., in *Nature*, November 17th, 1921, and to the "Guide to the Fossil Remains of Man" published by the British Museum (Natural History) in 1922.

but if it be admitted, as is now the trend of opinion, that Neanderthal man co-existed with higher types of man, before whom he became ultimately extinct, this difficulty disappears. Professor Keith now maintains that the Neanderthal type of tooth was actually further from the simian type than the teeth of Galley Hill man, and that the Neanderthal type must be regarded as, so to speak, side-tracked.

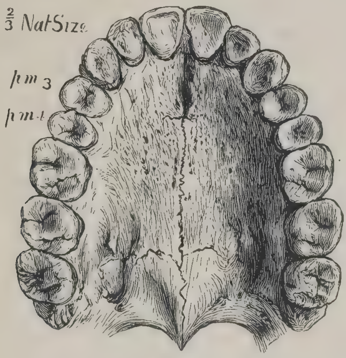

Fig. 324.—Upper jaw of a Kaffir. The oblique ridge of the upper molar is distinct, not only upon the first and second, but also upon the third, molar or wisdom tooth, which in this skull has the normal three roots well marked.

When we come to later periods there is not very much to be said about the teeth. In the Neolithic woman found in Essex all of the teeth were preserved, but they were much worn down, although the skeleton indicated that she was young. The teeth were regularly placed, and the palate is well formed, but the front teeth met in an edge-to-edge bite, allowing of the utmost freedom of lateral excursion. A large quantity of seeds of the blackberry and of the wild rose found

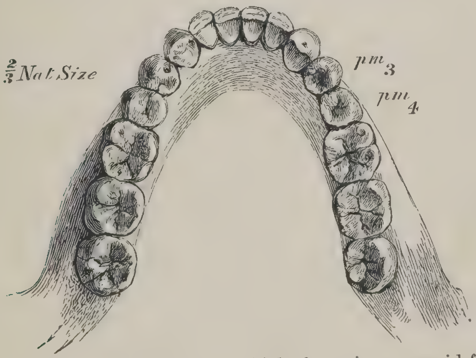

Fig. 325.—Lower jaw of a Kaffir, in which the quinquecuspid form of the first and third molars is well seen, it being somewhat less strongly indicated in the second molars.

within the ribs affords a clue to the nature of her diet. In the Tilbury skull, older, but also Neolithic, the back teeth had all been lost during life and their sockets rounded off; this is very unusual in ancient skulls. The remaining teeth were severely worn and their pulp cavities filled up by secondary dentine.

In general terms it may be said that the dentition of the lower races of living man differs from that of the higher in the following particulars: the arch is not so rounded, but is rather more square in front; the teeth are larger, and are disposed with greater regularity; the third molar has ample space to range with the other teeth, and there is often spare space behind it; it is a characteristic upper or lower molar, the pattern of its grinding surface (quadricuspid if it be an upper, quinquecuspid if it be a lower, tooth) and the disposition of its roots corresponding with the first and second molars, which do not greatly exceed it in size. Specimens of negro skulls may be found in which there is scanty room for the third molar, and in which consequently it is a little stunted in its development; on the other hand, plenty of well-formed and well-placed third molar teeth may be picked out of European mouths, though as a rule in the latter this tooth is smaller than the other molars, does not bear the characteristic pattern of cusps and grooves, has its roots connate, and is not very infrequently a mere rudimentary peg. The stunted development of the third molar would seem to be a consequence of want of space during its formative period; the upper third molar is especially apt to be cramped in this way.

There is some little evidence that this tooth is in process of disappearance from the jaws of civilised races; in anthropoid apes it is nearly or quite as large as the other molars, and shows no variability, whilst it comes into place almost simultaneously with the canine; in the lowest races of mankind the third molar appears to vary but little, is of large size, and is seldom misplaced; in highly civilised races it is very variable in size, form, and in the date of its appearance, is often misplaced, and is not uncommonly quite rudimentary. It seems to be a legitimate inference that a further modification of the race in the same direction will result in the disappearance of the wisdom tooth altogether. Some exception must, however, be taken to such general statements: thus the Esquimaux not uncommonly have the third molar teeth small and sometimes crowded out of place; and amongst the African races instances on the one hand of these teeth being small, and on the other of the existence of the fourth true molar, are to be met with.

Nevertheless, for the present, a case in which the third molar teeth are very small can hardly be called a typical well-developed European mouth.

It is stated by Regnault (11) that the upper incisors differ in the various races of mankind: in the white races their lateral borders are parallel, but they are divergent in negro races, so that the difference in width between the cutting edge and the neck is twice as great in the latter; this peculiarity exists also in the milk teeth, and is traceable in the canines of both dentitions. Moreover, it may be mentioned that in the milk dentitions the canines of man are very similar to those of the apes. The canines of lower races are generally very strong; and a slight diastema occasionally exists. Although man has ceased to use them as fighting weapons, yet there is a curious survival in an expression of the face, as is thus well put by Darwin: "He who rejects with scorn the belief that the shape of his own canines and their occasional great development in other men are due to our early progenitors having been provided with these formidable weapons will probably reveal by sneering the line of his descent. For though he no longer intends, nor has the power, to use these teeth as weapons, he will unconsciously retract his 'snarling muscles' (thus named by Sir C. Bell) so as to expose them ready for action, like a dog prepared to fight" ("Descent of Man," p. 127).

It has been pointed out by Sir William Turner that, besides the dental arches being both longer and broader in Australian skulls than in Europeans, the front teeth more often meet edge to edge instead of the lower passing well inside the upper incisors.

Europeans are sometimes divided into (i.) a brachycephalic dark type with rounded jaws, small teeth, and often tritubercular upper molars, and (ii.) a xanthocroic or fair type, who are dolicocephalic and taller. These have larger teeth, more square jaws, and less tendency to cusp reduction.

The cusp pattern of human molars has been a subject of interest to many observers, on account of its seeming to elucidate in some degree the problems of human descent.

Cusps of the upper molars according to Professor Osborn are to be thus interpreted*:—

Antero-internal = Protocone
Antero-external = Paracone } Primitive triangle or trigon.
Postero-external = Metacone

Postero-internal = Hypocone.

The homologies of the cusps of the lower molars are as follow:—

Antero-external = Protoconid } Two cusps of the primitive
Antero-internal = Metaconid } triangle.
Postero-external = Hypoconid
Postero-internal = Entoconid } Primitive heel.
Postero-mesial = Hypoconulid

The author commenced to make a record of the percentage of deviations in the cusps of the several races of mankind, but finding that Topinard (14) had already done so upon a very large series of skulls, and that the observations, so far as they had been carried, were in complete accord with his, desisted.

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* Topinard, however, interprets these differently. Morover, if Bolk's Dimer theory should prove to be correct, these terms will entirely lose their significance.—Ed.

Topinard, after rejecting all doubtful cases, includes in his record 595 human skulls, 120 anthropoid apes, and a very large number of lower apes.

He finds that $\underline{M_1}$ was quadricuspid, with a well-marked oblique ridge in 99 per cent. of human skulls taken without distinction of race, so that

$\underline{M_1}$ is constant in all races.

$\underline{M_2}$ had 4 cusps in 66 per cent. of all races.
,, $3\frac{1}{2}$,, ,, 16 ,, ,, ,, ,,
,, 3 ,, ,, 16 ,, ,, ,, ,,

(By $3\frac{1}{2}$ is meant three well-developed cusps with an indication of the fourth.)

$\underline{M_2}$ has the normal four cusps in 79 per cent. of Malays, 83 of New Caledonians and New Hebrideans, 78 of Melanesians, 73 of Australians and Tasmanians; but the percentage falls to 68 in Chinese and Japanese and to 58 in European, Semitic, and Egyptian skulls.

$\underline{M_3}$ had 4 cusps in 37 per cent. of all races
,, $3\frac{1}{2}$,, ,, 11 ,, ,, ,, ,,
,, 3 ,, ,, 39 ,, ,, ,, ,,
,, 2 ,, ,, 5 ,, ,, ,, ,,

and was totally irregular in 6 per cent.

$\underline{M_3}$ had four cusps in 72 per cent. of Melanesians, 69 of Egyptian groups, and only in 36 per cent. of European skulls. It had three cusps in 56 per cent. of Chinese and in 47 per cent. of negroes and Australians.

Thus, as he remarks, the third upper molars tend to be "disordered" in almost all races.

For lower molars he gives—

$\overline{M_1}$, 5 cusps in 82 per cent. of all races.
$4\frac{1}{2}$,, ,, 4 ,, ,, ,, ,,
4 ,, ,, 10 ,, ,, ,, ,,

Thus M_1 retains its type strongly, though not so absolutely as $\underline{M_1}$.

$\overline{M_2}$, 5 cusps in 24 per cent. of all races.
$4\frac{1}{2}$,, ,, 10 ,, ,, ,, ,,
4 ,, ,, 64 ,, ,, ,, ,,

$\overline{M_2}$ is distinctly a quadricuspid tooth, and is quinquecuspid less frequently than $\overline{M_1}$. It has the typical four cusps in 75 per cent. of Egyptians, in Europeans in 60 per cent., in negroes in 52 per cent., in Polynesians in 52 per cent., and in Japanese in 44 per cent.; whilst it has five cusps in 33 per cent. of Melanesian skulls, in 30 per cent. of Malays, and in 37 per cent. of Chinese and Japanese.

$\overline{M}_3$, 5 cusps in 46 per cent. of all races
4½ ,, ,, 6 ,, ,, ,, ,,
4 ,, ,, 31 ,, ,, ,, ,,

And $\overline{M}_3$ is very variable.

The race comparisons come out thus :—

In Europeans $\overline{M}_1$ is getting away from its original type, which occurs in only 61 per cent. Polynesians have the full five cusps in 91 per cent., Chinese and Japanese in 87 per cent., Melanesians in 86 per cent., negroes in 88 per cent., and Egyptians in 77 per cent.

From his observations he concludes that the teeth of man are in process of transformation, the lower molars tending towards a quadricuspid type with a crucial fissure, and the upper towards a tricuspid type.

In the lower it is the fifth cusp (which, from comparison with the teeth of apes, Topinard holds to primarily originate in the middle line, in a bifurcation of the posterior arm of the cross) which tends to displacement to the outer aspect of the crown more and more, until it disappears.

In the upper molars it is the postero-internal cusp which disappears, so that the tooth terminates posteriorly with the oblique ridge. This manner of suppression of cusps brings the human tricuspid molar into close resemblance to the trituberculate lemurine tooth ; but, as is set forth in the footnote below, Topinard by no means agrees with Osborn in the determination of the homologies of the cusps severally.*

It is therefore held by Cope to indicate that the upper molars of European races show a tendency to revert towards the Eocene trituberculate lemurine tooth.

When it is further reduced to two cusps, it is by the fusion into one of the antero- and postero-external cusps.

The range of variation in the size of the jaws of healthy and otherwise well-developed adults is great. Thus the smallest jaw (occurring in a man of stout build, above middle height) with which the author is acquainted measures in width only 1½ inch, and in length from back to front 1¾ inch ; while the largest (occurring in a gentleman of lesser stature, of Basque extraction moreover, which makes it the more striking †) measures no less than 2½ inches in width and 2¼ inches in length : and even larger dimensions are recorded in the

---

* Topinard holds that the antero-external cusp is the protocone *both in upper and lower molars*, therein differing from Osborn, and that the postero-external is the metacone, the paracone being absent in Primates, and both the internal cusps being secondary acquisitions. He states that in both jaws in development the antero-external is the first to appear, and long keeps a preponderance, the antero-internal following, then the postero-external, and much later the postero-internal.

† Magitot (" Bullet. de la Soc. Anthropol. de Paris," 1869) says : " Les Basques, par exemple, remarquables par la petitesse extrême de leurs dents."

Dental Cosmos of September, 1876, the width being taken between the centre of the alveolar borders at the position of the third molars, and the length being measured on a line drawn from the incisors to another line joining the two wisdom teeth.

On the whole, it must be said that there are fewer constant differences between the teeth of the various races of mankind than might have been *à priori* expected; in fact, it may almost be said that the teeth of savage man are such as we should look upon as an exceptionally perfectly formed set of teeth if we were to see them in the mouth of a European.

Flower (6) has investigated the relation of the size of the teeth to that of the skull very closely, with the result of bringing out certain race distinctions. As measures for comparison he takes the length of the cranio-facial organs, measured from the front edge of the occipital foramen to the naso-frontal suture, and the length from the front of the first premolar to the back of the third molar *in situ*. His "dental index" is arrived at thus:

$$\text{Dental Index} = \frac{\text{Length of Teeth} \times 100}{\text{Cranio-facial axis}}.$$

This gives figures ranging from 42 (microdont), 43 (mesodont), 44 and upwards (megadont).

As in females the skull is smaller, whilst the teeth are the same, a slightly higher index is arrived at for them.

The Microdont races are—

European.
British.
Egyptian.
Polynesian.

The Mesodont are—

Chinese.
American Indian.
Malays.
Negroes.

And the Megadont—

Melanesians.
Andamanese.
Australian.
Tasmanian.

As to this classification, it is to be remarked that the teeth of Polynesians are actually larger than those of Europeans, but the cranio-facial axis is of extreme length, so that the index is reduced; this is also the case with the American Indians, whilst the Andamanese are brought into the megadont series by the relative size of teeth to the basis cranii, though in this small people the teeth are actually small, considerations which diminish the value of the method.

The dental index of Megadont races being from 44 to 47, that of the chimpanzee is little more than the highest of these, namely, 47·9, whilst the orang rises to 55, and the gorilla to 54, but in the gibbon the index is as low as 41·7. It was, however, the opinion of the African traveller, Mr. Stanley, that the teeth of African races vary in accordance with the build of the individual, and particularly with the size of the jaws, such small races as the Somalis having small teeth. It does not appear, however, that these impressions are based upon actual exact measurement, but only upon general appearance. He mentions that many of the races who show no regard for cleanliness otherwise assiduously clean their teeth.

The account of the morphology of the teeth of the Primates has been thus briefly sketched in the preceding pages. The subject is one, however, which has recently attracted great attention, owing to the fact of the relative frequency with which the teeth have been found in the fossilised human remains. A considerable literature has therefore recently grown up, and the reader who wishes to study the subject more comprehensively is referred to the monographs on this subject by Bolk (2) and by de Terra (3).

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